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Calcareous sponges of the Western Indian Ocean and Red Sea

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Abstract

Past taxonomic studies of Western Indian Ocean and Red Sea Calcarea have been few and sporadic (e.g. Schuffner 1877, Jenkin 1908, Row 1909, Dendy 1913, 1916, Voigt *et al.* 2017, 2018). Nevertheless, approximately 70 species are known from these studies for the considered region, but the descriptions of the older records often lack sufficient details for reliable identification. We studied the Western Indian Ocean Calcarea collection kept in the Naturalis Biodiversity Center. Available specimens numbered 145, collected in the Red Sea, Seychelles, Maldives, Mayotte and Rodrigues, in addition to incidental samples from Oman, the Lakshadweep Islands, the Mozambique Channel, and Eastern South Africa. Using a combination of techniques (in situ and ‘on deck’ photography, detailed field notes, light microscopic studies and measurements, SEM microscopy, and selected DNA sequencing) we identified 45 species, divided over the two main classes Calcinea (24 spp.) and Calcaronea (21 spp.). Not all species could be definitely assigned to an already described or a new species, as seven remained qualified as ‘spec.’ or ‘aff.’ for reasons of insufficient material or lack of details of in situ habitus. Sixteen species appeared to be new to science: *Borojevia voigti* **sp.nov.**, *Borojevia tubulata* **sp.nov.**, *Borojevia pirella* **sp.nov.**, *Clathrina rodriguesensis* **sp.nov.**, *Clathrina maremeccae* **sp.nov.**, *Clathrina repens* **sp.nov.**, *Leucascus schleyeri* **sp.nov.**, *Leucetta sulcata* **sp.nov.**, *Ute insulagemmae* **sp.nov.**, *Leucandra pilula* **sp.nov.**, *Leucandra mozambi-quensis* **sp.nov.**, *Grantessa woerheidei* **sp.nov.**, *Sycettusa hirsutissima* **sp.nov.**, *Vosmaeropsis glebula* **sp.nov.**, *Paraleucilla erpenbecki* **sp.nov.**, and *Kebira tetractinifera* **sp.nov.** For a selection of the identified species from the Western Indian Ocean and the Red Sea (30 spp.), as well as from Indonesian material (22 spp.) published previously (see Van Soest & De Voogd 2015) we obtained sequences of the partial 28S gene of nuclear rDNA (C2–D2 region, cf. Voigt & Wörheide 2016). The sequences of the Western Indian Ocean and Red Sea species were used to assign these to genera and families based on a phylogenetic analysis using MEGA pack vs. 06.6 for Mac of the available dataset. The Indonesian sequences supplemented by partial 28S sequences taken from the Sponge Barcode Project website and the NCBI website were included in the phylogenetic analysis to confirm the assignments. The results were compared and discussed with additional information on regional Calcarea not represented in our material. The latter chapter yielded the discovery of a preoccupied name leading to *Sycon oscar* **nom.nov.** for a species described from Mauritius.

Key words: Porifera, Calcarea, new species, DNA barcodes, Aqaba, Jeddah, Maldives, Seychelles, Rodrigues

Introduction

Calcareaan biodiscovery, currently (Van Soest *et al.* 2012) estimated at about 8% of total sponge biodiversity, still lags behind the discovery of other sponge groups, with a poor historical effort and limited recent activities. After the late 19th century and early 20th century studies of Haeckel (1872), Schuffner (1877), Poléjaeff (1883), Von Lendenfeld (e.g. 1885), Dendy (e.g. 1891, 1913), Row (1909), Burton (e.g. 1930) and Brøndsted (e.g. 1931), there was a long pause in taxonomic activities for the group, with only sporadic efforts of Japanese scientists (numerous smaller papers by Hôzawa and Tanita). Inspired by Radovan Borojević, in the latter decades of the 20th century and the beginning of the present century, we now see a more continuous effort of taxonomists dedicated to Calcarea, with more integrated activities involving field observations and molecular approaches making the Calcarea better accessible to the scientific community. Nevertheless, compared to Demospongiae, the state of our knowledge of the diversity, distribution and ecology of Calcarea remains unsatisfactory. A case in point is the knowledge of Calcarea from the Western Indian Ocean and the Red Sea. Species are mostly known from old publications (Schuffner 1877, Jenkin 1908, Row 1909, Dendy 1913, 1916), and only very recently studies appeared on Red Sea (Voigt *et al.* 2017) and Maldives (Voigt *et al.* 2018) Calcarea presenting more expanded species knowledge, such as field photos, light microscopy, SEM observations and molecular sequence data. Our present study is intended to continue the efforts for expansion of the knowledge of Calcarea of the Western Indian Ocean and the Red Sea, following a similar study of Indonesian Calcarea (Van Soest & De Voogd 2015). One of us (NJDV) did a number of field studies in the Red Sea, Maldives, Mayotte and Rodrigues and this yielded a rich collection of Calcarea with in situ habitus photos, on deck photos, and selected fragments for DNA sequencing. This recent collection is complemented by older collecting activities in the Seychelles by RVS (1992–93), the Gulf of Aqaba (1998), and several incidental collections, to form a sizeable stock of specimens, which will be described below.

Material and methods

The Western Indian Ocean and Red Sea collection studied by us numbered 145 samples (one or more individuals of a species from the same location incorporated in a single unit and registered under a single collection number in the Naturalis Biodiversity Center at Leiden, The Netherlands) kept in 70% ethanol. The precise locality data and method of collecting of each sample is given with the description of each species below.

Frequent abbreviations are used in the tekst and captions of the figures:

RMNH = Rijksmuseum van Natuurlijke Historie, Leiden.

ZMA = Zoological Museum of Amsterdam, recently (2011) merged with the RMNH collection, but the acronym is maintained.

AQ = Gulf of Aqaba 1998 collection made by M. Wunsch, kept in the ZMA collection.

JED = Jeddah (Saudi Arabia) 2014 collection made by NJDV, kept in the RMNH collection.

MAY = Mayotte, 2013, collection made by NJDV, kept in the RMNH collection.

MAS = Maldives 2015 collection made by NJDV, kept in the RMNH collection.

NIOP-E = Seychelles Netherlands Indian Ocean Project (leg E) 1992–93 collection made by RVS, kept in the ZMA collection.

ROG = Rodrigues 2016 collection made by NJDV, kept in the RMNH collection.

The general locations from where our sponges originated is presented in the map of Fig. 1.

We studied the sponges by field observations, and for many recent samples also by photographing in situ, by photos on deck to record live color and post-collection artefacts, photos of preserved samples, light microscopy, SEM microscopy, and for selected specimen fragments by DNA extraction, PCR-ing, and sequencing. For most details of our methodology, we refer the reader to our Indonesian Calcarea article (Van Soest & De Voogd 2015). Light microscopic observations and measurements were done with a Leica DM5500 stacking microscope. SEM observations of sections and dissociated spicules were done with a JEOL Scanning Electron Microscope. Measurements of the spicules are based on minimum–average–maximum μm for 20 spicules of each separate

spicule type or actine of each studied individual, unless otherwise indicated (e.g. trichoxeas are very seldom complete, so often only a length range is given).

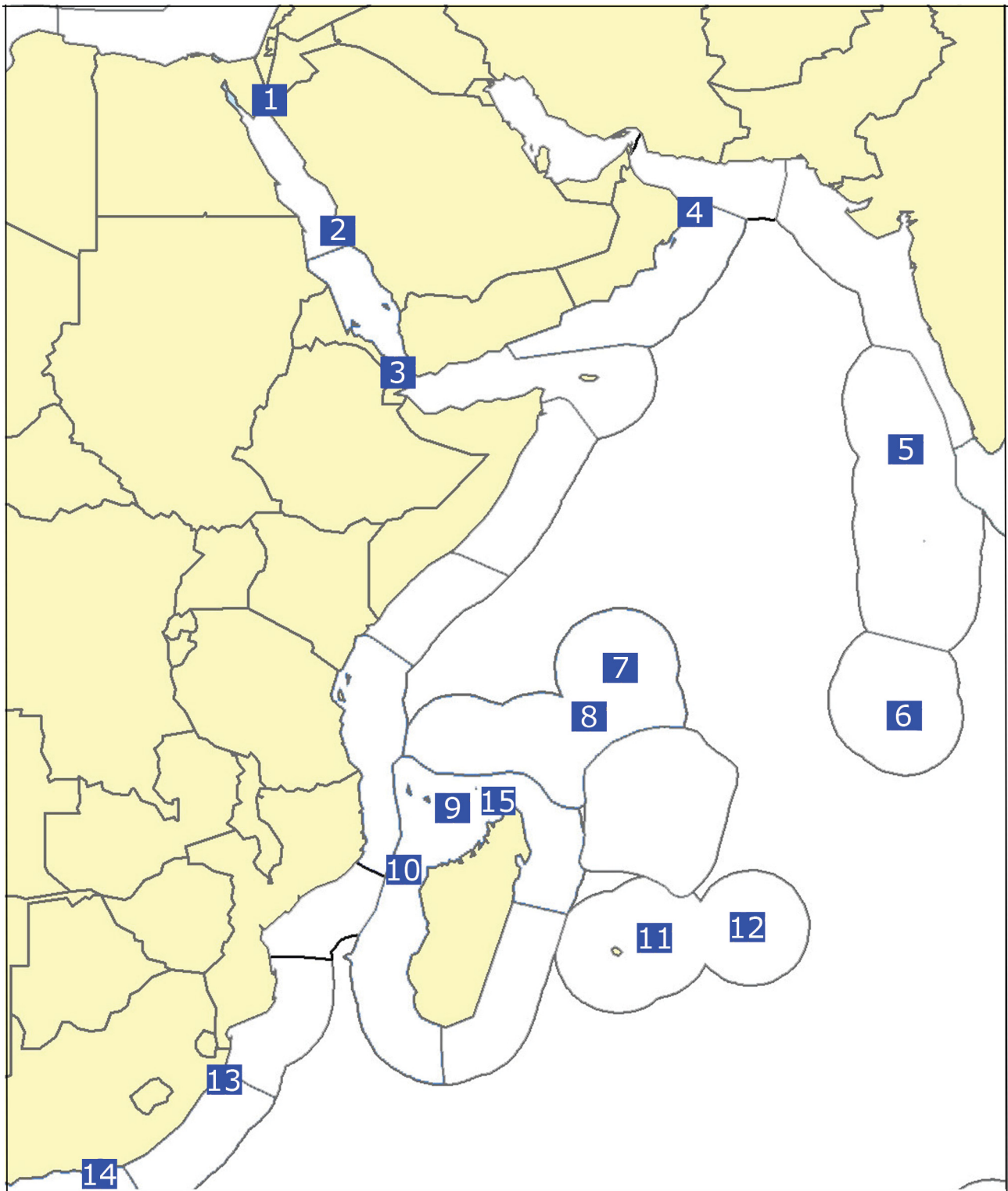


FIGURE 1. Marine Ecoregions in the Western Indian Ocean with localities (numbered blue squares) from where the studied calcareous sponges were obtained. 1, Israeli Red Sea, Gulf of Aqaba, 2, Saudi Arabian Red Sea, off Jeddah, 3, Eritrean Red Sea, Dahlak Archipelago, 4, Oman, Gulf of Arabia, 5, Maldives, 6, India, Lakshadweep, 7, Seychelles, Mahé region, 8, Seychelles, Amirantes, 9, Mayotte, 10, Mozambique Channel, 11, Mauritius, 12, Rodrigues, 13, South Africa, Kwazulu Natal, 14, South Africa, Port Elizabeth, 15, Nosy Be, Madagascar.

For the details of the DNA sequencing protocol we refer to that described in Van Soest *et al.* 2015, targeting the C2–D2 region of the nuclear ribosomal 28S gene, a.k.a. the ‘calcarea barcode’ (Voigt & Wörheide 2016). We sequenced not only an ample selection of Western Indian Ocean and Red Sea specimens described below, but we also sought to obtain sequences of Indonesian species, described recently by us (cf. Van Soest & De Voogd, 2015), to use these as comparison in case of closely related species, or as reference of species identity in cases of assumed conspecificity of Indonesian and Western Indian Ocean populations. Information on all the sequences used are presented in Table 1 (taxon name, museum registration number if known, locality, GenBank accession number, reference).

We used the 28S results for the narrow purpose of finding confirmation of our identifications of already known species, and corroboration of the genus and family assignment of species we found to be undescribed. We compared our sequences of the latter with sequences from the pool of regional species (i.e. Indo-West Pacific species) in order to be able to distinguish the described species from its congeners in the same region. We usually did not extend our comparisons to include species from other regions such as the Atlantic, Mediterranean or East Pacific regions, as we believe natural distribution patterns in Calcarea, as in other marine groups, are regionally restricted. In a few cases we had to deviate from this intent because of lack of regional sequences, in which case we compared our sequences with those from other regions or from groups further away phylogenetically. However, we were not aiming to contribute to reconstruction of the phylogeny of the Calcarea, as we believe that the short barcode-like gene 28S rRNA gene we employed is not sufficiently informative for that purpose.

The protocol we followed with the obtained sequences was: (1) assemble relevant fasta files belonging to separate subclasses Calcinea and Calcaronea, including one or more outgroup taxa, from our own sequence library, from Voigt *et al.*’s (2017) recent study and a few sequences awaiting study (courtesy of Oliver Voigt), and/or entries in the Sponge Barcoding Project site (<http://www.palaeontologie.geo.uni-muenchen.de/SBP/>), and from GenBank (<https://www.ncbi.nlm.nih.gov/nucleotide/>); (2) align the selected sequences using MEGApack vs. 06.6 for Mac’s (<http://www.megasoftware.net/megamac.php>) ClustalW option using all sequence positions; (3) trim the alignments resulting in sequence lengths of 442 (Calcinea) and 461 sites (Calcaronea); (4) reconstruct the phylogeny using the ML statistic method with the Bootstrap set at 1000 replicates; as Substitution Model we chose the Tamura-Nei model as Evolutionary Model, further parameters were used in their default settings, and we rooted the trees at midpoint.

In a few cases of closely related species and especially in case of new species we attempted to quantify molecular differences between sequences of a small group of species concerned by counting the shared and not-shared non-conserved sites of trimmed alignments visualized in MEGA’s display option of 100% toggled non-conserved sites. We refrained from presenting p-distance values because of MEGA’s unhelpful fine printed values, making the trees illegible.

Finally, in two cases in which 28S rRNA sequences were unavailable in the literature, but only ITS sequences, we generated ITS sequences of our own for comparison. These were not submitted to GenBank as they were only intended to support our statements on a few isolated genus identifications, while we targeted specifically the Calcarea barcode as our preferred gene.

We present our molecular taxonomic information including the phylogenetic trees prior to the (morphological) descriptions of the species to allow the reader to more easily check out our identifications and taxonomic decisions while moving through our paper.

The systematic classification below generally follows the Systema Porifera (Hooper & Van Soest 2002), chapters on Clathrinida (Borojević *et al.* 2002a), Leucosolenida (Borojević *et al.* 2002b), and Baerida (Borojević *et al.* 2000c). For Calcinea, the new genera described in Klautau *et al.* (2013) are adopted.

Results

The 145 samples were attributable to 45 species. Sixteen of these were found to be undescribed and are assigned to species new to science, seven species are not definitely assigned to species for reasons of insufficient material (in one case only a microscopic slide was available) or lack of details of in situ habitus, and their status is assigned as ‘spec.’ or ‘aff.’ The remaining twentytwo species were identified as already known. All species, new, already known, or indefinite, are fully described and illustrated. Sequence data of one or more specimens belonging to 30

Western Indian Ocean and Red Sea species were obtained to support decisions of their identity and affiliation. New sequences obtained from 22 Indonesian species and 4 from other regions are reported where relevant in the remarks of the species treated below. All these sequences have been submitted to GenBank, where they are available under their unique accession numbers (for these, see Table 1). Additionally, we imported 72 sequences from other sources (GenBank, SBP), 62 *Calcinea* and 10 *Calcaronea*.

Molecular Taxonomy

The sequences of which the relationships are presented in the *Calcinea* and *Calcaronea* phylogenetic trees are labeled by species name and GenBank accession number, and they have been listed alphabetically with supplementary information (museum registration numbers, localities and references) in Table 1. The *Calcinea* tree (Fig. 2) is of considerable length, making it necessary to present details in three subsidiary figures Figs 2A, 2B and 2C, the limits of which are indicated in the main Fig. 2 by the dotted lines. The *Calcaronea* tree (Fig. 3) is much shorter and is not further detailed. The numbers given for each branching node is the bootstrap value based on 1000 replicates. Sequences from Western Indian Ocean species treated morphologically in the present study are indicated by an asterisk.

In the *Calcinea* (Figs 2, 2A, 2B, 2C) most recognized species and genera are well-supported by high bootstrap values. Their detailed relationships are discussed in the remarks on the species treated systematically below. To provide confirmation of molecular affiliation of less well-represented genera and species, such as *Arturia adusta* (Wörheide & Hooper, 1999), *Leuclathrina translucida* Voigt *et al.*, 2018, *Borojevia* species, and *Leucaltis nodusgordii* (Poléjaeff, 1883) we included sequences of supposedly related genera and species, such as Indonesian *Arturia tubuloreticulosa* Van Soest & De Voogd, 2015, *A. angusta* (Van Soest & De Voogd, 2015 as *Ascaltis*), *Burtonulla sibogae* Borojević & Boury-Esnault, 1986, *Ascandra kakaban* Van Soest & De Voogd, 2015, *Levinella thalassae* Borojević & Boury-Esnault, 1987, *Soloneiscus hamatus* Voigt *et al.*, 2017, *Borojevia aspina* (Klautau *et al.*, 1994), *B. brasiliensis* (Solé-Cava *et al.*, 1991), *B. cerebrum* (Haeckel, 1872), as well as several *Borojevia* spp., *Leucascus flavus* Cavalcanti *et al.*, 2013, and *Ascaltis reticulum* (Schmidt, 1862). The sequence of the Indonesian species *Ernstia chrysops* Van Soest & De Voogd, 2015, which we included to supplement our regional set of *Ernstia* sequences, turned out to be grouped with *Ascandra*, *Levinella* and *Burtonulla*. To confirm the monophyly of our further *Ernstia* species, we included the Brazilian type species, *E. tetractina* (Klautau & Borojević, 2001) in our sequences. We added also two sequences of *Leuconia nivea* (Grant, 1826) (order Baerida) as outgroup sequences.

Two striking features are found in the *Calcinea* tree: (1) *Arturia* species appear to be non-monophyletic, with *A. sueziana* (Klautau & Valentine, 2003) widely divergent from *A. adusta*. In Fig. 2 we indicated these two *Arturia*'s as '*Arturia*' and *Arturia* s.s. This will be discussed below in our treatment of the genus *Arturia*. (2) The monophyly of our *Clathrina* species is seemingly compromised by our sequence of the Indonesian species *C. purpurea* Van Soest & De Voogd, 2015 which is grouped with some of the mentioned *Arturia* species in stead of the main group of *Clathrina*'s. However, the grouping is incidental, because there are large differences (up to 55 sites) between *Clathrina purpurea* and the *Arturia*'s with which it is grouped. We double-checked *C. purpurea* slides for the presence of rare tetractines, but none were found. The incidental grouping we obtained probably indicates that *Clathrina* shows considerable genetic diversity in the Indo-West Pacific region.

The *Calcaronea* tree (Fig. 3) contains fewer taxa than the *Calcinea* tree. The paucity of our gene sequences is reflected by the overall paucity of the partial 28S rRNA sequences available from other sources. The sequences are limited in number and comprise most often 18S sequences which are not alignable with our partial 28 sequences. Several of the represented genera and families in our sequence library appeared to be non-monophyletic, reflecting probably the poor representation of the 'barcode' sequences of this subclass. Next to GenBank sequences of the Indo-West Pacific region, we supplemented our sequences with Mediterranean *Paraleucilla* sp. and two *Sycon* species from Western Europe, in an attempt to obtain molecular support for our genus assignments. We added three *Calcinean* sequences (*Pericharax orientalis*) as outgroup. More details are provided in the Remarks of the various species presented below.

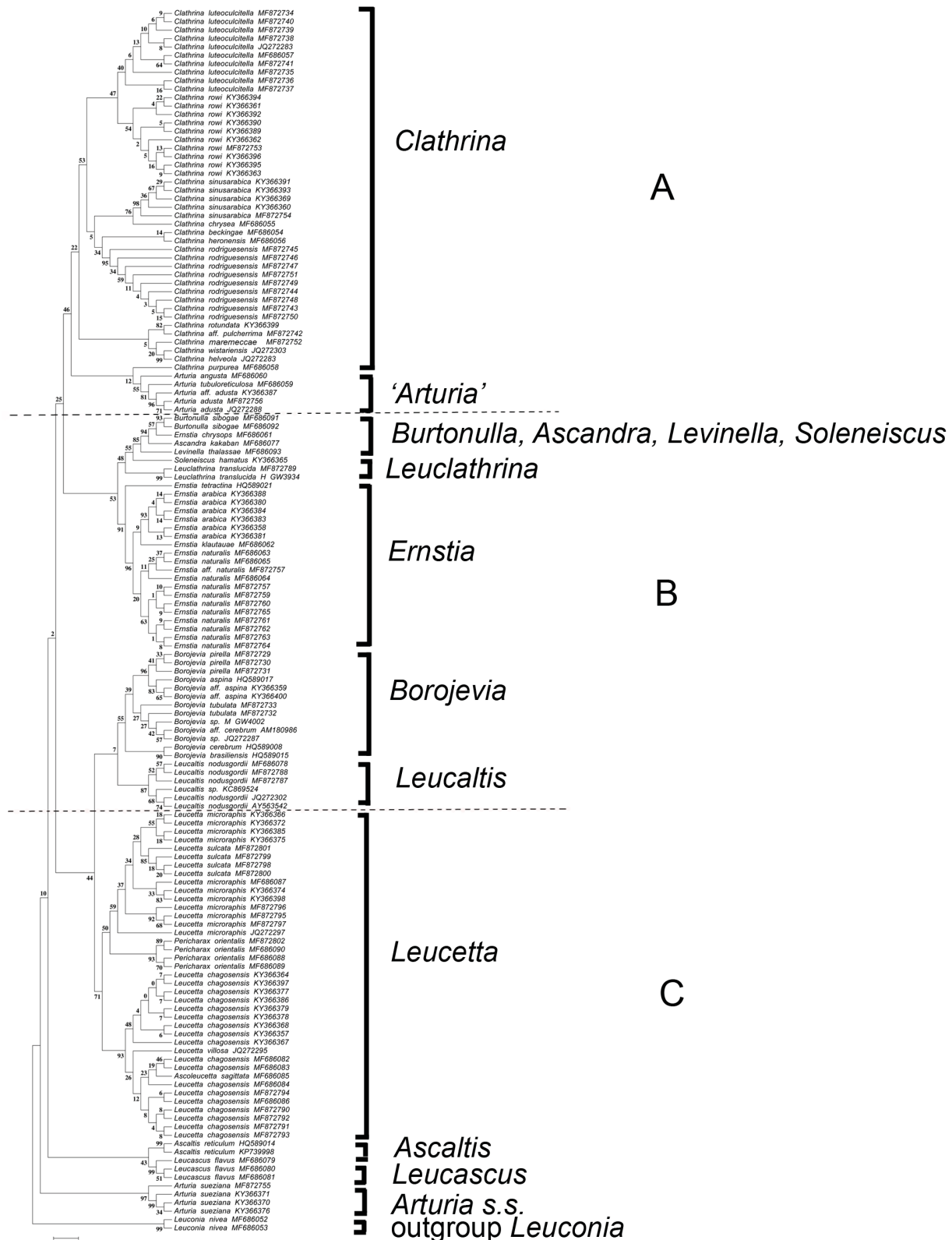


FIGURE 2. Maximum-likelihood tree based on analysis of sequences of the partial 28S gene (C2–D2 region, comprising 442 sites) of Western Indian Ocean Calcinea newly generated by the Naturalis Biodiversity Center and sequences additionally obtained from GenBank, the Sponge Barcode Project and from Oliver Voigt (München) from the Red Sea, Indonesia, Australia, and a few sequences from other parts of the world, to demonstrate the affiliation of the compared species. Please note that *Arturia* sequences do not appear in the same clade, indicating *Arturia* is non-monophyletic. Numbers at the root of clades are bootstrap values of 1000 replicates. Since the high number of sequences were difficult to read in detail, we subdivided the present tree in three detailed sections 2A, 2B, and 2C.

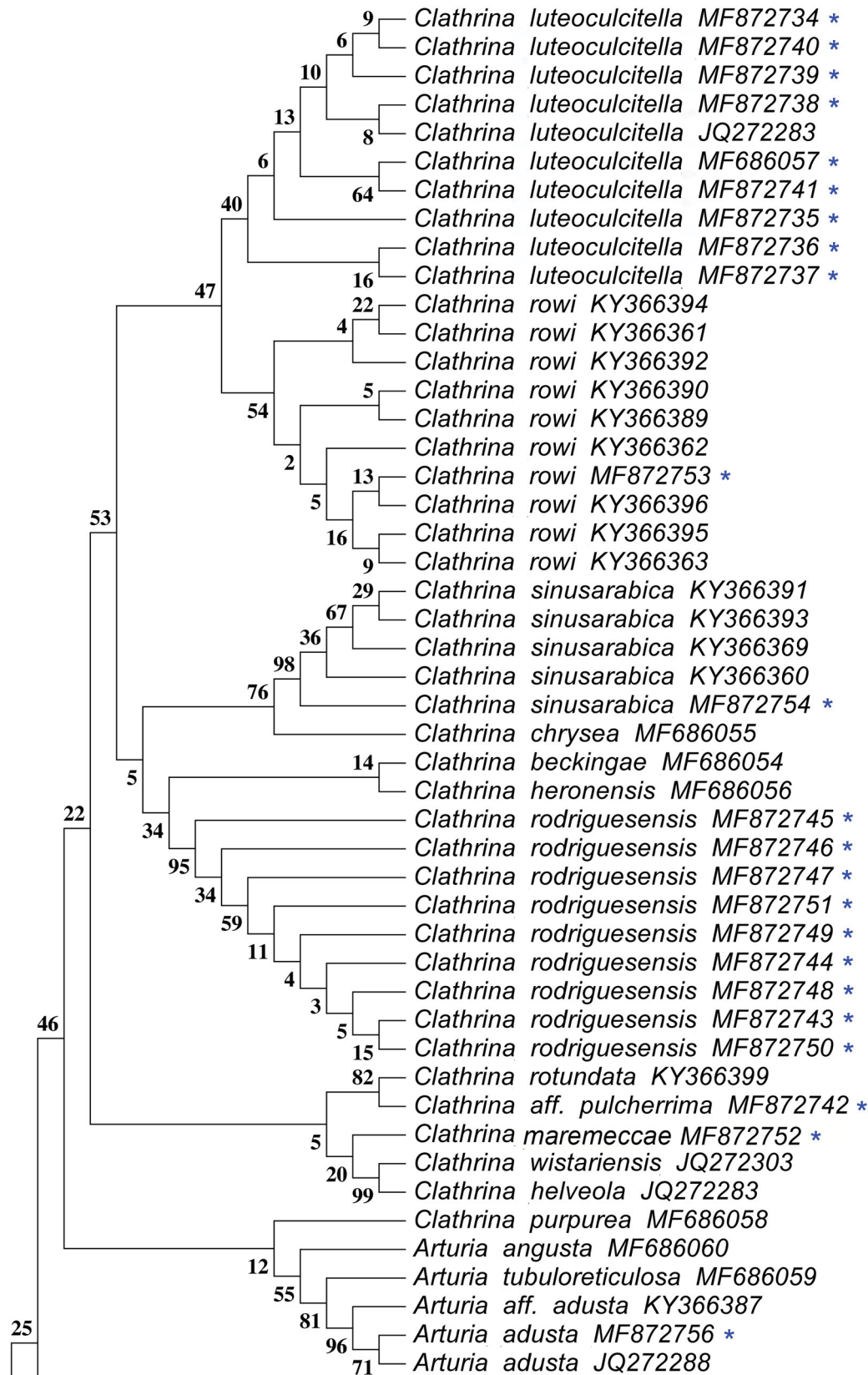


FIGURE 2A. Upper section of Calcinea tree shown in Figure 2, comprising *Clathrina* and ‘*Arturia*’ species.

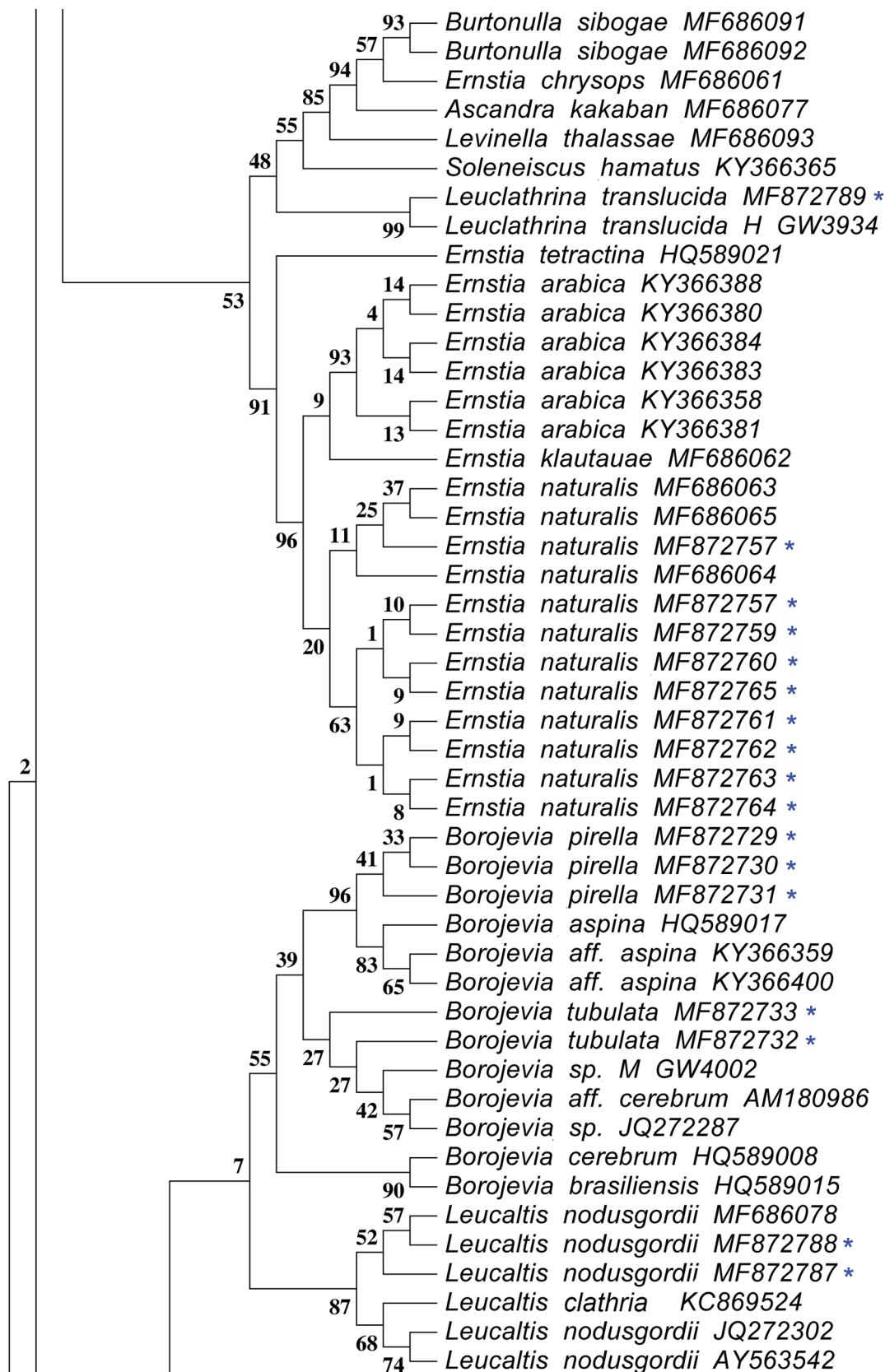


FIGURE 2B. Middle section of *Calcinea* tree shown in Figure 2, comprising *Burtonulla*, *Ascandra*, *Levinella*, *Leuclathrina*, *Ernstia*, *Borojevia* and *Leucaltis* species.

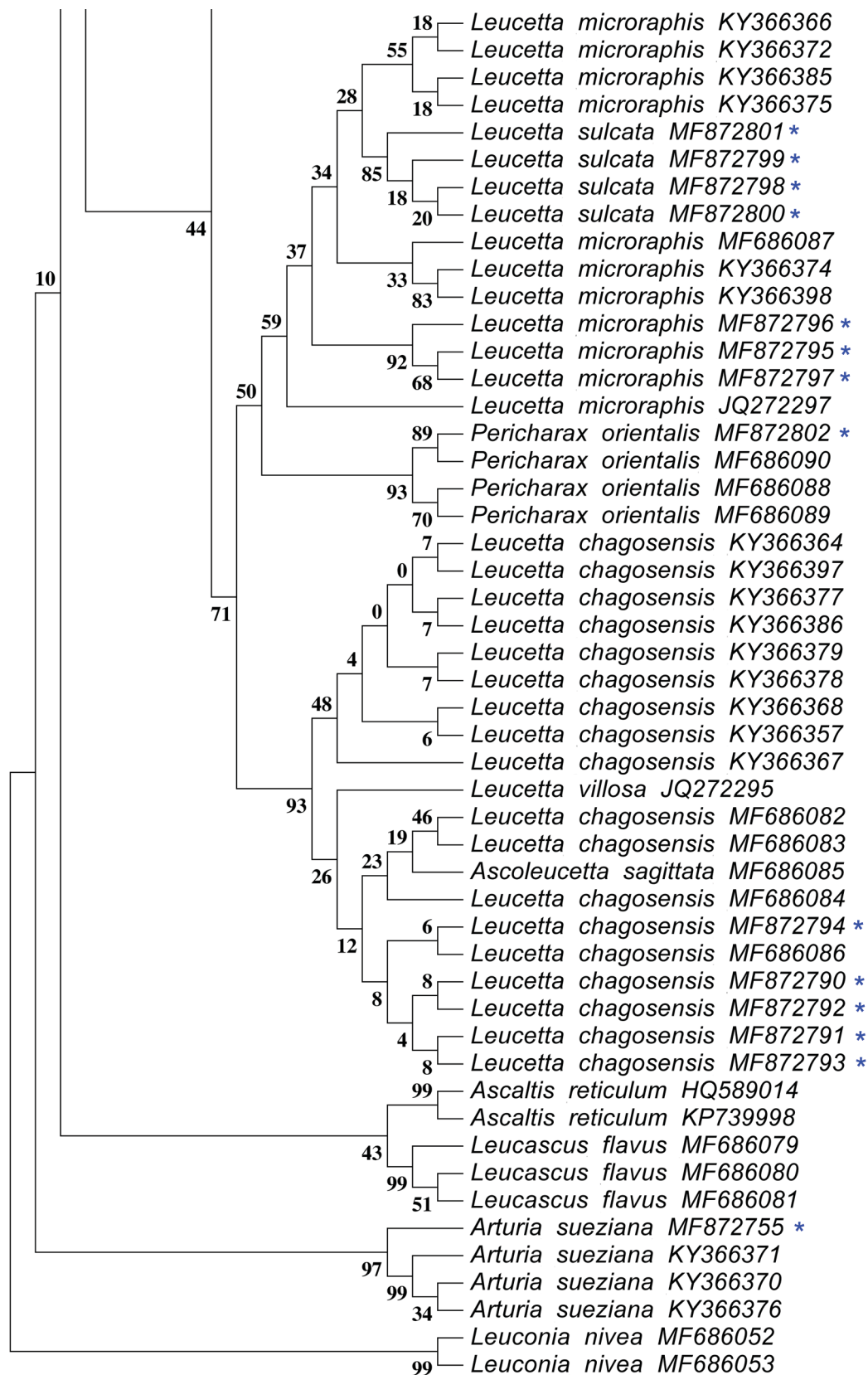


FIGURE 2C. Lower section of Calcinea tree shown in Figure 2, comprising *Leucetta*, *Pericharax*, *Ascaltis*, *Leucascus* and *Arturia* species.

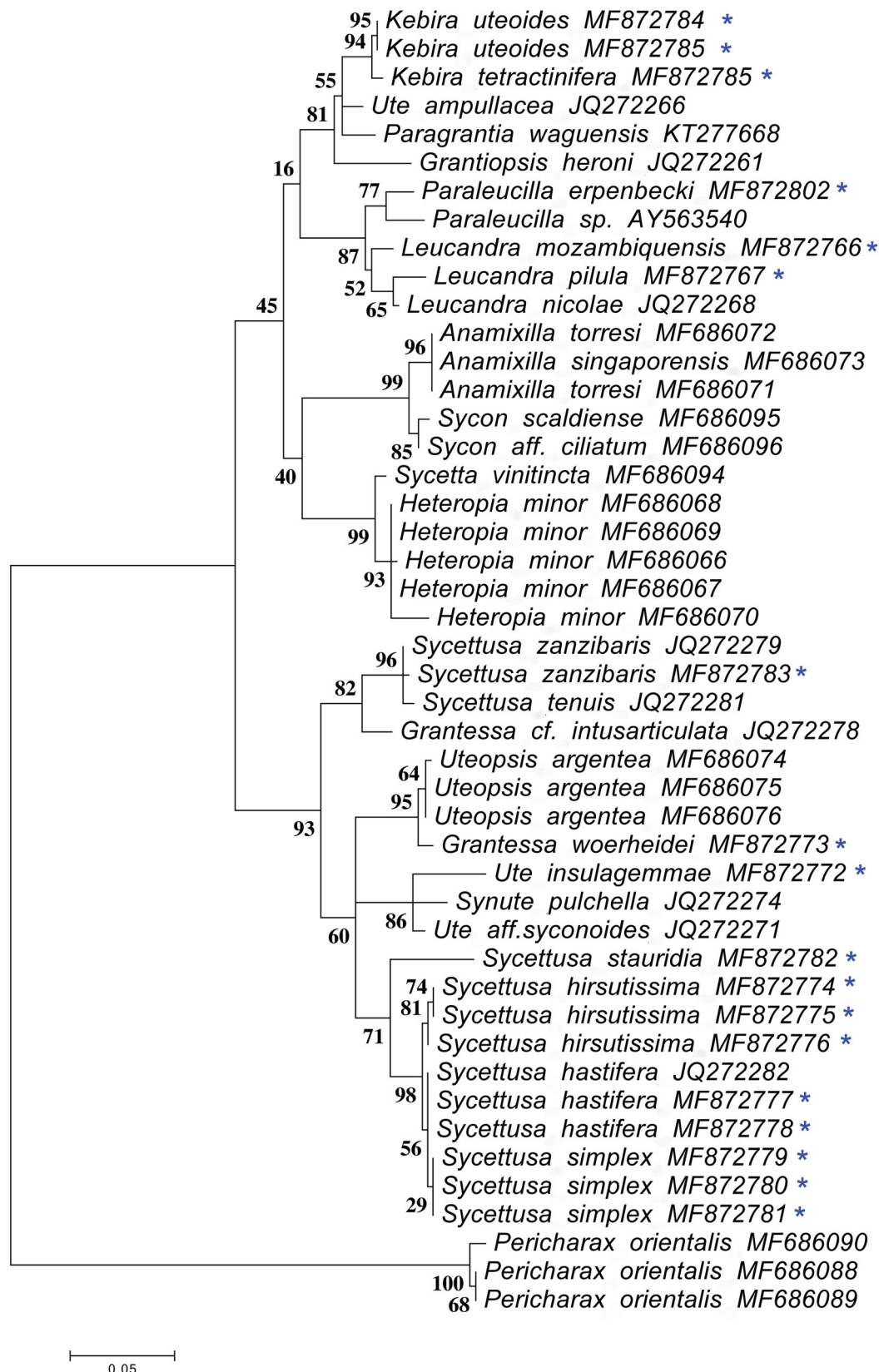


FIGURE 3. Maximum-likelihood tree based on analysis of sequences of the partial 28S gene (C2–D2 region, comprising 461 sites) of Western Indian Ocean Calcareous Sponges newly generated by the Naturalis Biodiversity Center and sequences additionally obtained from GenBank, the Sponge Barcode Project and from Oliver Voigt (München) from the Red Sea, Indonesia, Australia, and a few sequences from other parts of the world, to demonstrate the affiliation of the compared species. Numbers at the root of clades are bootstrap values of 1000 replicates.

TABLE 1. Sequences used for phylogenetic analysis used in our text and figures. The sequences are arranged alphabetically with the entries of the taxa in the combination as given in the references and/or GenBank. Columns comprise Taxon, voucher registration numbers (Reg.nr.), Locality, accession numbers (GenBank acc.nr.), where applicable followed by Sponge Barcoding Database numbers (SBDSeq), and Reference.

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Anamixilla singaporensis</i>	RMNH.POR.9350	Singapore	MF686073	Van Soest & De Voogd, 2015
<i>Anamixilla torresi</i>	RMNH.POR.6572	Indonesia	MF686072	Van Soest & De Voogd, 2015
<i>Anamixilla torresi</i>	RMNH.POR.6612	Indonesia	MF686071	Van Soest & De Voogd, 2015
<i>Arturia adusta</i>	QMG313665	Australia	JQ272288/SBDSeq1727	Wörheide & Hooper, 1999
<i>Arturia adusta</i>	ZMA.POR.10612	Seychelles	MF872756	this paper
<i>Arturia sueziana</i>	RMNH.POR.10112	Maldives	MF872755	this paper
<i>Arturia sueziana</i>	SNB-BSPG GW3168	Red Sea	KY366376	Voigt et al. 2017
<i>Arturia sueziana</i>	SNB-BSPG GW3121	Red Sea	KY366371	Voigt et al. 2017
<i>Arturia sueziana</i>	SNB-BSPG GW3120	Red Sea	KY366370/SBDSeq1795	Voigt et al. 2017
<i>Arturia tubuloreticulosa</i>	RMNH.POR.5547	Indonesia	MF686059	Van Soest & De Voogd, 2015
<i>Ascaltis</i> (= ' <i>Arturia</i> ') <i>angusta</i>	ZMA.POR.08221a	Indonesia	MF686060	Van Soest & De Voogd, 2015
<i>Ascaltis reticulum</i>	UFRJPOR6258 (DC19)	Medit.	HQ589014	Rossi et al. 2011
<i>Ascaltis reticulum</i>	UFRJPOR6870/PMR13739	Medit.	KP739998	Klautau et al. 2016
<i>Ascaltis</i> (= <i>Borojevia</i>) <i>spec.</i>	QMG313824/OV-2012	Australia	JQ272287	Voigt et al. 2012
<i>Ascandra kakaban</i>	RMNH.POR.1696	Indonesia	MF686077	Van Soest & De Voogd, 2015
<i>Ascoleucetta sagittata</i>	ZMA.POR.13283	Indonesia	MF686085	Van Soest & De Voogd, 2015
<i>Borojevia</i> aff. <i>aspina</i>	KAUMM-1	Red Sea	KY366359	Voigt et al. 2017
<i>Borojevia</i> aff. <i>aspina</i>	SMF11637	Red Sea	KY366359	Voigt et al. 2017
<i>Borojevia pirella</i> sp.nov.	RMNH.POR.11622A_1	Rodrigues	MF872729	this paper
<i>Borojevia pirella</i> sp.nov.	RMNH.POR.11622A_2	Rodrigues	MF872730	this paper
<i>Borojevia pirella</i> sp.nov.	RMNH.POR.11622B	Rodrigues	MF872731	this paper
<i>Borojevia tubulata</i> sp.nov.	RMNH.POR.10158	Maldives	MF872732	this paper

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Borojevia tubulata</i> sp.nov.	ZMA.POR.12435	Seychelles	MF872733	this paper
<i>Borojevia</i> spec.	M GW4002	Maldives		Voigt, pers. comm.
<i>Burtonulla sibogae</i>	RMNH.POR.9195	Indonesia	MF686091	Van Soest & De Voogd, 2015
<i>Burtonulla sibogae</i>	RMNH.POR.9345	Indonesia	MF686092	Van Soest & De Voogd, 2015
<i>Clathrina</i> (= 'Arturia') <i>adusta</i>	SMF11618	Red Sea	KY366387	Voigt et al. 2017
<i>Clathrina</i> (= 'Arturia') aff. <i>adusta</i>	M GW3957	Maldives		Voigt pers.comm.
<i>Clathrina</i> (= <i>Borojevia</i>) <i>aspina</i>	UFRJPOR5495(DC25)	Brazil	HQ589017	Klautau et al. 2013
<i>Clathrina beckingae</i>	RMNH.POR.4482	Indonesia	MF686054	Van Soest & De Voogd, 2015
<i>Clathrina</i> (= <i>Borojevia</i>) <i>brasiliensis</i>	URFJPOR5214 (DC21)	Brazil	HQ589015	Rossi et al. 2011
<i>Clathrina</i> (= <i>Borojevia</i>) <i>cerebrum</i>	UFRJPOR6322 (DC11)	Medit.	HQ589008	Rossi et al. 2011
<i>Clathrina</i> (= <i>Borojevia</i>) aff. <i>cerebrum</i>	QMG313824	Australia	AM180986	Dohrmann et al. 2006
<i>Clathrina chrysea</i>	ZMA.POR.16165	Indonesia	MF686055	Van Soest & De Voogd, 2015
<i>Clathrina helveola</i>	QMG313680	Australia	JQ272283/SBDSseq1729	Voigt et al. 2012
<i>Clathrina heronensis</i>	RMNH.POR. 4499	Indonesia	MF686056	Van Soest & De Voogd, 2015
<i>Clathrina luteoculcitella</i>	ZMA.POR.08657	Indonesia	MF686057	Van Soest & De Voogd, 2015
<i>Clathrina luteoculcitella</i>	RMNH.POR.11623	Rodrigues	MF872735	this paper
<i>Clathrina luteoculcitella</i>	RMNH.POR.11641_1	Rodrigues	MF872738	this paper
<i>Clathrina luteoculcitella</i>	RMNH.POR.11641_2	Rodrigues	MF872739	this paper
<i>Clathrina luteoculcitella</i>	RMNH.POR.11686	Rodrigues	MF872740	this paper
<i>Clathrina luteoculcitella</i>	RMNH.POR.11687	Rodrigues	MF872734	this paper
<i>Clathrina luteoculcitella</i>	RMNH.POR.11703_1	Rodrigues	MF872736	this paper
<i>Clathrina luteoculcitella</i>	RMNH.POR.11703_2	Rodrigues	MF872737	this paper
<i>Clathrina luteoculcitella</i>	ZMA.POR.17438	Oman	MF872741	this paper
<i>Clathrina luteoculcitella</i>	QMG313684	Australia	JQ272283/SBDSseq1730	Voigt et al.2012
<i>Clathrina maremeccae</i> sp.nov.	RMNH.POR.9662	Red Sea	MF872752	this paper

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Clathrina</i> aff. <i>pulcherrima</i>	ZMA.POR.22408c	Mozambique	MF872742	this paper
<i>Clathrina purpurea</i>	RMNH.POR.6625	Indonesia	MF686058	Van Soest & De Voogd, 2015
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11662_1	Rodrigues	MF872744	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11662_2	Rodrigues	MF872748	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11670	Rodrigues	MF872749	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11671_1	Rodrigues	MF872745	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11671_2	Rodrigues	MF872746	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11694	Rodrigues	MF872743	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	RMNH.POR.11705	Rodrigues	MF872747	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	ZMA.POR. 11282	Seychelles	MF872751	this paper
<i>Clathrina rodriguesensis</i> sp.nov.	ZMA.POR. 12096	Seychelles	MF872750	this paper
<i>Clathrina rotundata</i>	SMF11636	Red Sea	KY366399	Voigt et al. 2017
<i>Clathrina rowi</i>	RMNH.POR.10002	Red Sea	MF872753	this paper
<i>Clathrina rowi</i>	SMF11507	Red Sea	KY366361	Voigt et al. 2017
<i>Clathrina rowi</i>	SMF11532	Red Sea	KY366362	Voigt et al. 2017
<i>Clathrina rowi</i>	SMF11629	Red Sea	KY366390	Voigt et al. 2017
<i>Clathrina rowi</i>	SMF11632	Red Sea	KY366394	Voigt et al. 2017
<i>Clathrina rowi</i>	SMF11633	Red Sea	KY366395	Voigt et al. 2017
<i>Clathrina rowi</i>	SMF11634	Red Sea	KY366396	Voigt et al. 2017
<i>Clathrina rowi</i>	KAUMM-2	Red Sea	KY366363	Voigt et al. 2017
<i>Clathrina rowi</i>	KAUMM-3	Red Sea	KY366389	Voigt et al. 2017
<i>Clathrina rowi</i>	KAUMM-4	Red Sea	KY366392	Voigt et al. 2017
<i>Clathrina sinusarabica</i>	RMNH.POR.10003	Red Sea	MF872754	this paper
<i>Clathrina sinusarabica</i>	SMF11630	Red Sea	KY366391	Voigt et al. 2017
<i>Clathrina sinusarabica</i>	SMF11631	Red Sea	KY366393	Voigt et al. 2017

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Clathrina sinusarabica</i>	SNSB-BSPG-GW3025	Red Sea	KY366369	Voigt et al. 2017
<i>Clathrina sinusarabica</i>	KAUMM-5	Red Sea	KY366360	Voigt et al. 2017
<i>Clathrina (=Ernstia) tetractina</i>	UFRJPOR5183	Brazil	HQ589021	Rossi et al. 2011
<i>Clathrina wistariensis</i>	QMG313663	Australia	JQ272303/SBDSseq1726	Voigt et al. 2012
<i>Ernstia arabica</i>	SMF11578	Red Sea	KY366380	Voigt et al. 2017
<i>Ernstia arabica</i>	SMF11627	Red Sea	KY366388	Voigt et al. 2017
<i>Ernstia arabica</i>	SMF11627	Red Sea	KY366388/SBDSseq1800	Voigt et al. 2017
<i>Ernstia arabica</i>	SNS-BSPG GW1130	Red Sea	KY366358	Voigt et al. 2017
<i>Ernstia arabica</i>	KAUMM-6	Red Sea	KY366381	Voigt et al. 2017
<i>Ernstia arabica</i>	KAUMM-7	Red Sea	KY366383	Voigt et al. 2017
<i>Ernstia arabica</i>	KAUMM-8	Red Sea	KY366384	Voigt et al. 2017
<i>Ernstia chrysops</i>	RMNH.POR.1773	Indonesia	MF686061	Van Soest & De Voogd, 2015
<i>Ernstia klautauae</i>	RMNH.POR.9341	Indonesia	MF686062	Van Soest & De Voogd, 2015
<i>Ernstia naturalis</i>	RMNH.POR.5000	Indonesia	MF686064	Van Soest & De Voogd, 2015
<i>Ernstia naturalis</i>	RMNH.POR.9342	Indonesia	MF686063	Van Soest & De Voogd, 2015
<i>Ernstia naturalis</i>	RMNH.POR.9343	Indonesia	MF686065	Van Soest & De Voogd, 2015
<i>Ernstia naturalis</i>	RMNH.POR.11612	Rodrigues	MF872762	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11614	Rodrigues	MF872761	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11629	Rodrigues	MF872764	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11633	Rodrigues	MF872759	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11660	Rodrigues	MF872765	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11667	Rodrigues	MF872760	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11702	Rodrigues	MF872763	this paper
<i>Ernstia naturalis</i>	RMNH.POR.11719	Rodrigues	MF872758	this paper
<i>Ernstia naturalis</i>	RMNH.POR.8444	Mayotte	MF872757	this paper

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Grantessa cf. intusarticalata</i>	SNSB-BSPG GW974	Australia	JQ272278/SBDSSeq1746	Voigt et al. 2017
<i>Grantessa woerheidei</i> sp.nov.	RMNH.POR.9586	Red Sea	MF872773	this paper
<i>Grantiopsis heroni</i>	QMG313670	Australia	JQ272261/SBDSSeq1738	Voigt et al. 2012
<i>Heteropia minor</i>	RMNH.POR.1872	Indonesia	MF686070	Van Soest & De Voogd, 2015
<i>Heteropia minor</i>	RMNH.POR.2164	Indonesia	MF686069	Van Soest & De Voogd, 2015
<i>Heteropia minor</i>	RMNH.POR.3603	Indonesia	MF686068	Van Soest & De Voogd, 2015
<i>Heteropia minor</i>	RMNH.POR.9194	Indonesia	MF686067	Van Soest & De Voogd, 2015
<i>Heteropia minor</i>	RMNH.POR.9349	Indonesia	MF686066	Van Soest & De Voogd, 2015
<i>Kebira tetractinifera</i> sp.nov.	ZMA.POR.15245	South Africa	MF872786	this paper
<i>Kebira uteoides</i>	RMNH.POR.9563	Red Sea	MF872784	this paper
<i>Kebira uteoides</i>	RMNH.POR.9664	Red Sea	MF872785	this paper
<i>Leucaltis clathria</i> (= <i>L. nodusgordii</i>)	QMG316022	Australia	JQ272302	Voigt et al. 2012
<i>Leucaltis clathria</i> (= <i>L. nodusgordii</i>)	QMG316022	Australia	AY563542	Voigt et al. 2012
<i>Leucaltis nodusgordii</i>	RMNH.POR.1772	Indonesia	MF686078	Van Soest & De Voogd, 2015
<i>Leucaltis nodusgordii</i>	ZMA.POR.12436	Seychelles	MF872787	this paper
<i>Leucaltis nodusgordii</i>	ZMA.POR.12443	Seychelles	MF872788	this paper
<i>Leucaltis spec.</i> (= <i>L. clathria</i>)	P10x28	Panama (Car.)	KC869524	Thatcher et al. 2013
<i>Leucandra mozambiquensis</i> sp.nov.	ZMA.POR.22408b	Mozambique	MF872766	this paper
<i>Leucandra nicolae</i>	QMG313672	Australia	JQ272268	Voigt et al. 2012
<i>Leucandra pilula</i>	ZMA.POR.10528	Seychelles	MF872767	this paper
<i>Leucascus flavus</i>	RMNH.POR.2279	Indonesia	MF686080	Van Soest & De Voogd, 2015
<i>Leucascus flavus</i>	RMNH.POR.9346	Indonesia	MF686081	Van Soest & De Voogd, 2015
<i>Leucascus flavus</i>	RMNH.POR.9347	Indonesia	MF686079	Van Soest & De Voogd, 2015
<i>Leucetta chagosensis</i>	RMNH.POR.10141	Maldives	MF872794	this paper
<i>Leucetta chagosensis</i>	RMNH.POR.11656	Rodrigues	MF872792	this paper

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Leucetta chagosensis</i>	RMNH.POR.11657_1	Rodrigues	MF872790	this paper
<i>Leucetta chagosensis</i>	RMNH.POR.11657_2	Rodrigues	MF872793	this paper
<i>Leucetta chagosensis</i>	RMNH.POR.11658	Rodrigues	MF872791	this paper
<i>Leucetta chagosensis</i>	SNSB-BSPG GW1122	Red Sea	KY366357	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SNSB-BSPG GW2973	Red Sea	KY366364	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SNSB-BSPG GW3039	Red Sea	KY366367	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SNSB-BSPG GW3052	Red Sea	KY366368	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SNSB-BSPG GW3052(2)	Red Sea	KY366368	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SNSB-BSPG GW3178	Red Sea	KY366377	Voigt et al. 2017
<i>Leucetta chagosensis</i>	KAUMM-9	Red Sea	KY366378	Voigt et al. 2017
<i>Leucetta chagosensis</i>	KAUMM-10	Red Sea	KY366379	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SMF11598	Red Sea	KY366386	Voigt et al. 2017
<i>Leucetta chagosensis</i>	SMF11635	Red Sea	KY366397	Voigt et al. 2017
<i>Leucetta chagosensis</i>	RMNH.POR.1792	Indonesia	MF686086	Van Soest & De Voogd, 2015
<i>Leucetta chagosensis</i>	RMNH.POR.1923	Indonesia	MF686084	Van Soest & De Voogd, 2015
<i>Leucetta chagosensis</i>	RMNH.POR.1652	Indonesia	MF686082	Van Soest & De Voogd, 2015
<i>Leucetta chagosensis</i>	RMNH.POR.9349	Indonesia	MF686083	Van Soest & De Voogd, 2015
<i>Leucetta microraphis</i>	RMNH.POR.8318	Mayotte	MF872796	this paper
<i>Leucetta microraphis</i>	RMNH.POR.8341	Mayotte	MF872795	this paper
<i>Leucetta microraphis</i>	RMNH.POR.8717	Madagascar	MF872797	this paper
<i>Leucetta microraphis</i>	RMNH.POR.6610	Indonesia	MF686087	Van Soest & De Voogd, 2015
<i>Leucetta microraphis</i>	SMF11581	Red Sea	KY366385	Voigt et al. 2017
<i>Leucetta microraphis</i>	SNSB-BSPG-GW3028	Red Sea	KY366366	Voigt et al. 2017
<i>Leucetta microraphis</i>	SNSB-BSPG-GW3144	Red Sea	KY366372	Voigt et al. 2017
<i>Leucetta microraphis</i>	SNSB-BSPG-GW3163	Red Sea	KY366374	Voigt et al. 2017

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Leucetta microraphis</i>	SNSB-BSPG-GW3164	Red Sea	KY366375	Voigt et al. 2017
<i>Leucetta microraphis</i>	KAUMM-12	Red Sea	KY366398	Voigt et al. 2017
<i>Leucetta microraphis</i>	QMG313659	Australia	JQ272297/SBDSseq1723	Voigt et al. 2012
<i>Leucetta sulcata</i> sp.nov.	RMNH.POR.11639_1	Rodrigues	MF872798	this paper
<i>Leucetta sulcata</i> sp.no	RMNH.POR.11639_2	Rodrigues	MF872799	this paper
<i>Leucetta sulcata</i> sp.nov.	RMNH.POR.11643	Rodrigues	MF872801	this paper
<i>Leucetta sulcata</i> sp.nov.	RMNH.POR.11645	Rodrigues	MF872800	this paper
<i>Leucetta villosa</i>	QMG313662	Australia	JQ272295/SBDSseq1725	Voigt et al. 2012
<i>Leuclathrina translucida</i>	RMNH.POR.10072	Maldives	MF872789	this paper
<i>Leuconia nivea</i>	ZMA.POR.19813	Helgoland	MF686052	this paper
<i>Leuconia nivea</i>	ZMA.POR.19816	Helgoland	MF686053	this paper
<i>Levinella thalassae</i>	ZMA.POR.18150	N.Atlantic	MF686093	Van Soest et al. 2007
<i>Paragrantia waguensis</i>	RMNH.POR.9317	Japan	KT277668	Van Soest et al. 2015
<i>Paraleucilla erpenbecki</i> sp.nov.	ZMA.POR.22409c	Mozambique	MF872728	this paper
<i>Paraleucilla</i> spec.	MM-2004	Medit.	AY563540	Manuel et al. 2004
<i>Pericharax orientalis</i>	RMNH.POR.10157	Maldives	MF872802	this paper
<i>Pericharax orientalis</i>	RMNH.POR.5259	Indonesia	MF686090	Van Soest & De Voogd, 2015
<i>Pericharax orientalis</i>	RMNH.POR.8551	Indonesia	MF686089	Van Soest & De Voogd, 2015
<i>Pericharax orientalis</i>	ZMA.POR.17412	Indonesia	MF686088	Van Soest & De Voogd, 2015
<i>Soleniscus hamatus</i>	SNSB-BSPG-GW2975	Red Sea	KY366365	Voigt et al. 2017
<i>Sycetta vinitincta</i>	RMNH.POR.1873	Indonesia	MF686094	Van Soest & De Voogd, 2015
<i>Sycettusa hastifera</i>	RMNH.POR.9659	Red Sea	MF872777	this paper
<i>Sycettusa hastifera</i>	ZMA.POR.13443	Red Sea	MF872778	this paper
<i>Sycettusa hastifera</i>	SNS-BSPG GW893	Red Sea	JQ272282/SBDSseq1743	Voigt et al. 2017
<i>Sycettusa hirsutissima</i> sp.nov.	RMNH.POR.9588_1	Red Sea	MF872775	this paper

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TABLE 1. (Continued)

Taxon	Reg.nr.	Locality	GenBank acc.nr.	Reference
<i>Sycettusa hirsutissima</i> sp.nov.	RMNH.POR.9588_2	Red Sea	MF872776	this paper
<i>Sycettusa hirsutissima</i> sp.nov.	RMNH.POR.10004	Red Sea	MF872774	this paper
<i>Sycettusa simplex</i>	RMNH.POR.10154_1	Maldives	MF872779	this paper
<i>Sycettusa simplex</i>	RMNH.POR.10154_2	Maldives	MF872780	this paper
<i>Sycettusa simplex</i>	ZMA.POR.12446	Seychelles	MF872781	this paper
<i>Sycettusa</i> cf. <i>simplex</i> (= <i>S. zanzibar</i>)	ZMA.POR.11566	Seychelles	JQ272279	Voigt et al. 2017
<i>Sycettusa stauridia</i>	ZMA.POR.13664	Seychelles	MF872782	this paper
<i>Sycettusa temis</i>	QMG313685	Australia	JQ272281/SBDS	Seq1740
<i>Sycettusa zanzibar</i>	ZMA.POR.11568	Seychelles	MF872783	this paper
<i>Sycon</i> aff. <i>ciliatum</i>	ZMA.POR.19809	North Sea	MF686096	this paper
<i>Sycon</i> <i>scaldiense</i>	ZMA.POR.21237	North Sea	MF686095	this paper
<i>Synute pulchella</i>	WAMZ1404	Australia	JQ272274	Voigt et al. 2012
<i>Ute ampullacea</i>	QMG313669	Australia	JQ272266/SBDS	Seq1737
<i>Ute insulagemmae</i> sp.nov.	ZMA.POR.11562	Seychelles	MF872772	this paper
<i>Ute</i> aff. <i>syconoides</i>	QMG313694	Australia	JQ272271	Voigt et al. 2012
<i>Uteopsis argentea</i>	RMNH.POR.1871	Indonesia	MF686074	Van Soest & De Voogd, 2015
<i>Uteopsis argentea</i>	RMNH.POR.2598	Indonesia	MF686075	Van Soest & De Voogd, 2015
<i>Uteopsis argentea</i>	RMNH.POR.6593	Indonesia	MF686076	Van Soest & De Voogd, 2015

Systematic descriptions

Class Calcarea Bowerbank, 1864

Subclass Calcinea Bidder, 1898

Order Clathrinida Hartman, 1958

Family Clathrinidae Minchin, 1900

Remarks. Since the Systema Porifera classification of the order Clathrinida (see Borojević *et al.* 2002a), substantial changes of the contents of the family Clathrinidae have been proposed (Klautau *et al.* 2013) and elaborated (Klautau *et al.* 2016). The genus *Clathrina* Gray, 1867 has been subdivided into five distinct genera, *Arturia* Azevedo *et al.*, 2017 (pro *Arthuria* Klautau *et al.*, 2013), *Borojevia* Klautau *et al.*, 2013, *Ernstia* Klautau *et al.*, 2013, *Brattegardia* Klautau *et al.*, 2013, and *Clathrina* s.s.. The only other genus of the family recognized in the Systema Porifera, genus *Guancha* Miklucho-Maclay, 1868, has been subsumed into *Clathrina* s.s., because its type species *Guancha blanca* Miklucho-Maclay, 1868 has been transferred to *Clathrina* sensu Klautau *et al.*, 2013. One former *Guancha* species, *G. tetela* Borojević & Peixinho, 1976 was recently reassigned to a new genus, *Nicola* Condór-Luján & Klautau, 2016. The classification is still in a flux, as it was recently revealed that the name *Arthuria* was preoccupied by two Mollusca genera (Polyplacophora and Pulmonata). It has just now been replaced by *Arturia*, but it is still complicated by our discovery (see below) that *Arturia* is probably not a monophyletic genus.

The family contents are also possibly overlapping with other families of the order Clathrinida, awaiting an overhaul based on a phylogenetic analysis of molecular sequence data. We will here follow the classification as presented in Klautau *et al.* 2013, with above listed recognized genera presented in alphabetical order (*Brattegardia* excepted as it was not represented in our material).

Below we will use the word ‘tubuli’ to describe the anastomosed ascon tubes of Clathrinidae species to avoid confusion with the tubes of tubular habitus in some species with a pseudoatrium. We maintain the term ‘water-collecting tubes’ for those wider tubuli leading to oscules.

Genus *Arturia* Azevedo *et al.*, 2017

Remarks. Our Calcinea phylogeny (Figs 2, 2A, 2C) shows a peculiar discrepancy in the affiliation of the two species of *Arturia* we found in our collection of Calcarea from the Western Indian Ocean. *A. sueziana* (Klautau & Valentine, 2003) is grouped on its own in Figs 2 and 2C outside any of the Calcinean genus and family clades, whereas *A. adusta* (Wörheide & Hooper, 1999) ended up close to the main group of *Clathrina* species. We investigated which of the two species is closest to the type species of *Arturia*, i.e. *A. hirsuta* (Klautau & Valentine, 2003), by downloading the available GenBank 18S sequences of *Arturia* species, because apart from Voigt *et al.*’s (2017) 28S rRNA sequences and our own, there are no other *Arturia* sequences of that gene in GenBank. The 18S sequences of the type species (accession numbers KC843431 & KC985143), of *A. sueziana* (KY366410), of *Clathrina adusta* (AM180962), of two additional unnamed *Arturia* species (KC985141 & KC985142), of *Ernstia tetractina*, of *Clathrina sinusarabica* Klautau & Valentine, 2003 (KY366407), and of *Leucetta floridana* Haeckel, 1872 (KC843456) were analyzed with the MEGA package. The result (not shown) clearly confirmed that *A. sueziana* is close to the type species *A. hirsuta* and the two unnamed *Arturia*, near *Leucetta floridana*, and that *Clathrina adusta* did not group with these, but ended up separately and nearer to *Clathrina sinusarabica* and *Ernstia tetractina*. In our Fig. 2A it is demonstrated that *Arturia adusta* is joined by the Indonesian *Arturia tubuloreticulosa* Van Soest & De Voogd, 2015 and *Arturia angusta* (Van Soest & De Voogd, 2015) (transferred here, but originally as *Ascaltis*). We are not proposing a new genus for this second *Arturia* group, but we confirm Voigt *et al.*’s (2017) suggestion that the *Ernstia*-*Arturia* relationships need to be analyzed further, not only molecularly, but also morphologically. The morphological characters provided by Klautau *et al.* (2013) fail to give sufficient support for recognition of three *Clathrina*-like generic taxa with tetractines, *Ernstia*, *Arturia* s.s. and ‘*Arturia*’.

Arturia sueziana (Klautau & Valentine, 2003)

Figures 4a–f

Clathrina canariensis var. *compacta*; Row 1909: 184 (not: Schuffner, 1877).

Clathrina sueziana Klautau & Valentine, 2003: 43, fig. 35.

Arturia sueziana; Voigt *et al.* 2017: 15, figs 9a–h.

Material examined. RMNH Por. 9537, Saudi Arabia, Jeddah, near Thuwal, Al Bilut (Rose Reef), 22.309861°N 38.886472°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. THU03/JED022, 7 November 2014; RMNH Por. 10112, Maldives, Faafu Atoll, Free Climbing, 3.066583°N 72.923028°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. MAD06/MAS067, 18 February 2015.

Description. Relatively massive, rounded to conical cormi of tightly anastomosed tubuli, converging at the upper surface to a few wide, tapering oscular (water-collecting) tubes (Figs 4a–c). Overall size is up to 3 x 1.5 x 1.5 cm, tubuli diameters 0.2–0.5 mm, water-collecting tubes up to 8 mm in diameter. Color pale yellow or dirty white.

Aquiferous system. Asconoid.

Skeleton. (Figs 4d) The tubule wall has two or more layers of overlapping triactines and tetractines, the latter with the apical actines protruding in the tubar lumen. The ratio of triactines vs. tetractines was 7:1 in RMNH 9537 and 7.5:1 in RMNH 10112, a clear predominance of triactines.

Spicules. (Figs 4e–f) Triactines and tetractines; trichoxeas were observed in a very low frequency in all samples, invariably broken.

Triactines (Figs 4e) predominantly equiradiate and equiangular, but a few are sagittal with paired actines wing-shaped. Actines conical, actine lengths in the various specimens:

RMNH Por. 9537: 96–128.8–146 x 8.5–10.5–14.5 µm (paired and unpaired actines of sagittal triactines of approximately same length).

RMNH Por. 10112: 48–111–153 x 6–11.8–15 µm (ditto).

Tetractines (Fig. 4f) with basal triradiate system predominantly equiradiate, occasionally sagittal, with apical actines smooth, thinner, but up to the same length of the actines of the basal triradiate system. Basal actines conical, actine sizes in the various specimens:

RMNH Por. 9537: 36–119.4–147 x 4–10.7–14 µm, apical actines 54–104.4–164 x 4–4.9–7 µm.

RMNH Por. 10112: 64–115–156 x 6–10.2–13 µm, apical actines 32–84–153 x 4–5.7–8.5 µm.

Distribution and ecology. Red Sea (Suez; Thuwal Reefs, near Jeddah), Maldives, in reef localities under overhangs.

Remarks. This is the first time the species has been recorded from outside the Red Sea. The habitus and spicular characters of the Jeddah and Maldives specimens in our collection are so close that conspecificity seems obvious. There are some spicule size differences with the Suez holotype (tetractines are only up to 98 µm, apical actines of the tetractines are only up to 63 µm). In Voigt *et al.*'s (2017) specimens there was a clear presence of trichoxeas (also mentioned in the holotype, quite rare in the present material). However, trichoxeas are notoriously variable in Clathrinidae, and the habitus and overall characters match with all three records.

We obtained a partial 28S rRNA sequence for the Maldives specimen (sequencing of our Red Sea specimen failed). The Maldives sequence ended up in the same clade together with three Red Sea sequences from Voigt *et al.* (2017) in a high bootstrap support (cf. Fig. 2C). Nevertheless, the identical Red Sea sequences together differed substantially from the Maldives sequence (in more than 10 sites), indicating a possible specific difference, which may become evident when more studies of Western Indian Ocean localities have been made.

Arturia darwinii (Haeckel, 1872) was reported from Zanzibar by Jenkin (1908) as *Clathrina*. It was described as bright lemon-yellow in color and the tri- and tetractines had basal actines 60–120 x 12–16 µm, with the apical actines of the tetractines having the same length but thinner (8 µm). These measurements overlap with the above given data on *A. sueziana*. The species is also reported from the Mozambique Channel by Barnes & Bell (2002), but no description was given. The type locality of *A. darwinii* is Java, Indonesia (cf. Van Soest & De Voogd 2015), but Haeckel also reported specimens from the Red Sea. The distinction between *A. darwinii* and *A. sueziana* remains to be further established.

All the above presented discrepancies with the holotype of *A. sueziana* support Klautau & Valentine's (2003) statement that *A. sueziana* is a complex of species.

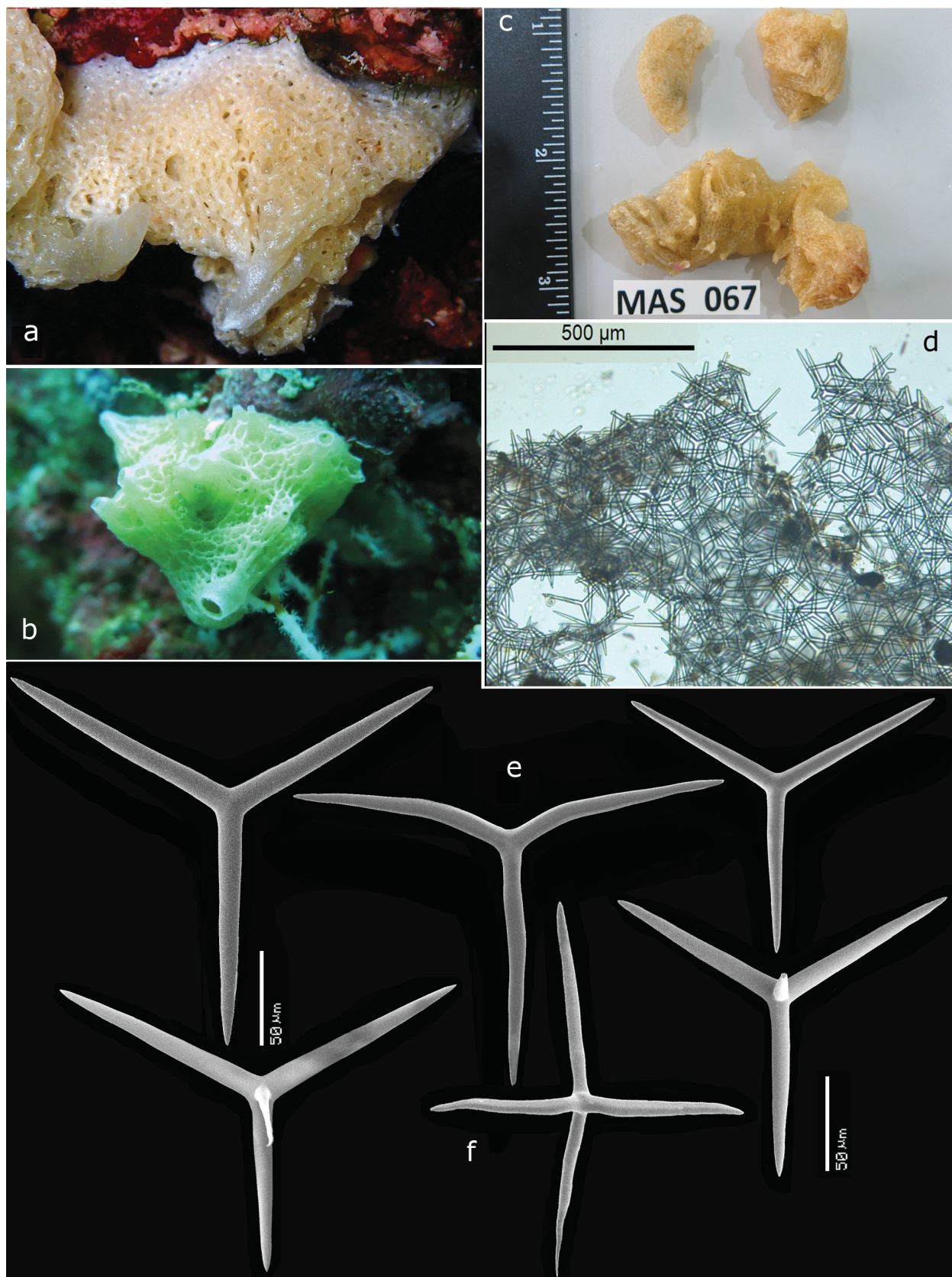


FIGURE 4. *Arturia sueziana* (Klautau & Valentine, 2003) habitus in situ, on deck and preserved, a, RMNH Por. 9537, in situ at Thuwal Reefs, near Jeddah, Saudi Arabia, b, RMNH 10112, in situ at Maldives, Faafu Atoll, c, RMNH Por. 10112 on deck, (in situ photos N.J. de Voogd), d, light microscopic image of skeleton of RMNH Por. 10112 from the Maldives, e–f, SEM images of spicules of RMNH Por. 10112 from the Maldives, e, triactines, f, tetractines.

***Arturia* (?) *adusta* (Wörheide & Hooper, 1999)**

Figures 5a–e

Clathrina adusta Wörheide & Hooper, 1999: 865, figs 4D–H.

Ernstia adusta; Klautau *et al.* 2013: 12.

Arthuria adusta; Voigt & Wörheide 2016: 61

Clathrina aff. *adusta*; Voigt *et al.* 2017: 5, fig. 3.

Material examined. ZMA Por. 10612, Seychelles, La Digue Island, S coast, 4.3833°S 55.8333°E, depth 2–8 m, snorkling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 735/32, 23 December 1992.

Description. Cormus a small cushion (Fig. 5a), about 1 x 0.7 cm in lateral expansion, thickness 2–4 mm. Life color is unknown, in alcohol it is orange-yellow. Structure compact, made up of tightly anastomosed thin tubuli. No visible oscules. Consistency soft.

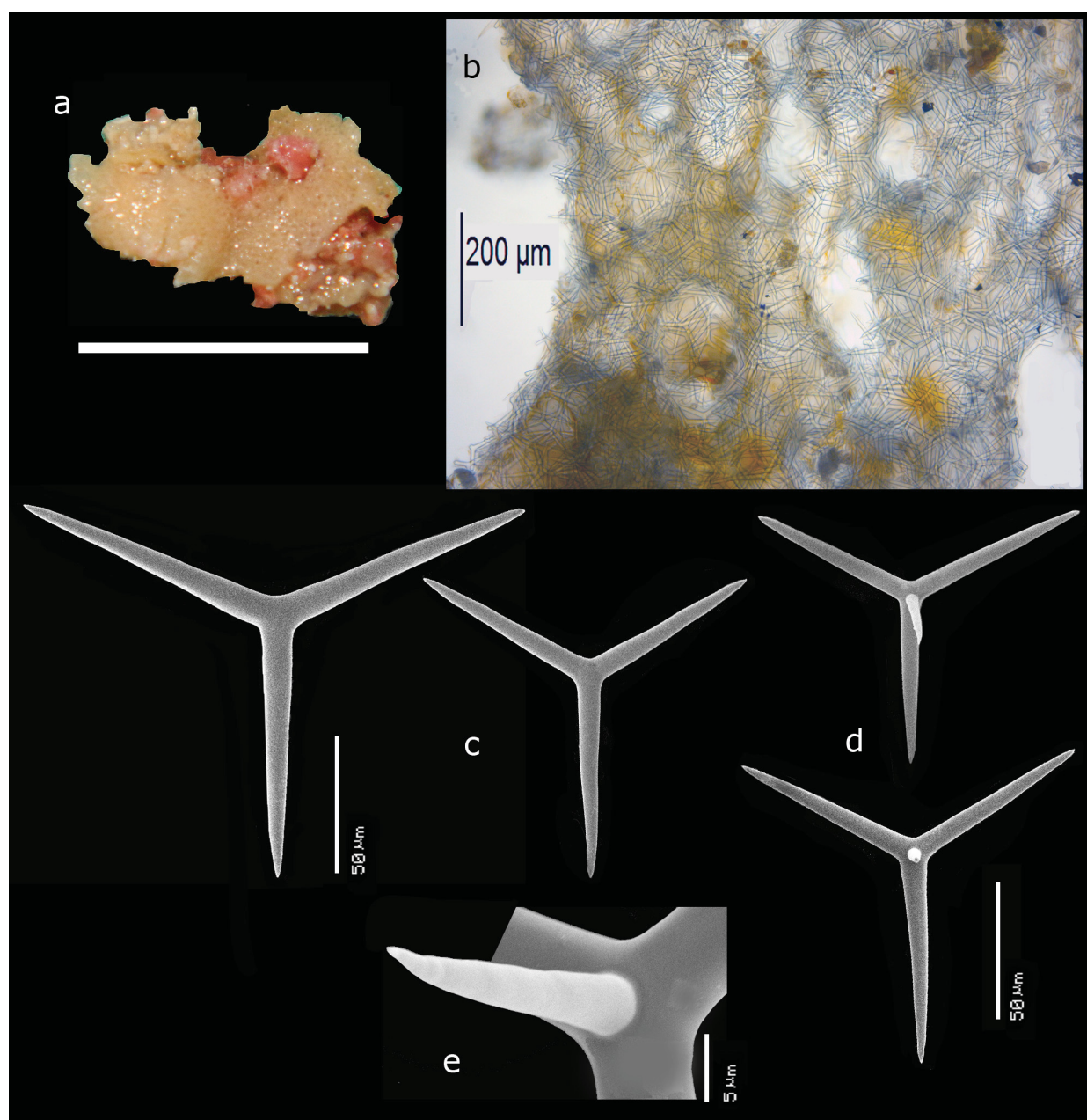


FIGURE 5. *Arturia* (?) *adusta* (Wörheide & Hooper, 1999), ZMA Por. 10612, from the Seychelles, La Digue island, a, preserved habitus (scale bar = 1 cm), b, light microscopic image of cormus showing tight anastomosis of tubuli, c–e, SEM images of the spicules, c, triactines, d, tetractines, e, detail of apical actine of tetractine.

Aquiferous system. Asconoid.

Skeleton. (Fig. 5b) Wall of tubuli thin, consisting of one-two spicule layers with a prominence of triactines. The apical actines of the tetractines are protruding into the tubule lumina.

Spicules. (Figs 5c–e) Triactines and tetractines, the latter present in clearly smaller numbers. No distinct trichoxeas were found.

Triactines (Figs 5c) equiradiate and equiangular, with conical actines, some verging toward tripod-shape; actine sizes 48–76–108 x 6.5–8.7–12 μm .

Tetractines (Figs 5d) of similar shape and size to the triactines, actines of the basal triradiate system 54–73–87 x 6.5–7.6–9.5 μm ; apical actines (Fig. 5e) smooth, straight, sometimes with a slightly upturned apex, 39–55–78 x 3–5.9–7.5 μm .

Distribution and ecology. Egyptian Red Sea (Voigt *et al.* 2017), Seychelles, NE Australia, on reefs in shallow depths.

Remarks. We base our identification largely on the sequence we obtained for our species, which ended up in a clade together with Voigt *et al.*'s (2012) Australian sequence of *Arturia adusta* and Voigt *et al.*'s (2017) Red Sea *Clathrina* aff. *adusta* (see his fig. 3). Klautau *et al.* (2013) had earlier assigned *Clathrina adusta* to *Ernstia*. Voigt & Wörheide (2016) discovered that this species falls outside the *Ernstia* clade and suggested that it should go to *Arturia*. We confirm that *C. adusta* is not an *Ernstia*, but with Voigt *et al.* (2017) we agree that assignment of *C. adusta* to *Arturia* s.s. is probably not correct, because *Arturia sueziana* and the type species of the genus *Arturia*, did not group in the same clade as *C. adusta* (see discussion above).

The present specimen resembles the type of Wörheide & Hooper (1999), although the white color cannot be affirmed. In glutaraldehyde the color of the type apparently changed to dark brown. Actine sizes 90–142 x 12–20 μm , more robust than in the Seychelles specimen, but overlapping. Voigt *et al.*'s (2017) record from the Red Sea mentioned actine sizes of 66–73 x 9–10 μm , more similar to our specimen than to the type. The three sequences for these specimens differed only in a few sites (two between the type and the Seychelles specimen, three between the type and the Red Sea specimen).

Genus *Borojevia* Klautau *et al.*, 2013

Borojevia voighti sp. nov.

Figures 6a–d, 7a–d

Material examined. Holotype, ZMA Por. 13444, Israel, pillar container port, Gulf of Aqaba, depth 5 m, scuba, coll. M. Wunsch, field nr. AQ65, 5 July 1998.

Description. Cormus (Figs 6a,a1) a greyish white cushion (Fig. 6a1, arrow), brighter white in alcohol (Fig. 6a), made up of tightly anastomosed thin tubuli. Oscules small, about 2 mm diameter, flush with the surface. Size of entire specimen is 2.5 x 2 x 1 cm.

Aquiferous system. Asconoid.

Skeleton. (Figs 6b–d) Tubuli walls consist of one–two layers of triactines and tetractines. Apical actines of tetractines protruding into the tubar lumen (Fig. 6d).

Spicules. (Figs 7a–d) Triactines and tetractines, about equal in number. Some trichoxea-like spicules appear present in the spicule slides.

Triactines (Fig. 7a) equiradiate and equiangular, with conical actines measuring 42–89–117 x 7–8.7–11 μm .

Tetractines (Figs 7b–d) shaped similarly and of approximate equal size. Apical actines straight, equal in length or longer than the actines of the basal triradiate system, tapering to a thin point (Fig. 7b), occasionally entirely smooth (Fig. 7c left), but usually provided with a few small spines (Figs 7c right). Actines of the basal triradiate system 32–61–105 x 4–6.8–10 μm , apical actines 24–67–138 x 3–5.1–7 μm .

?Trichoxeas (Fig. 7d), up to 300+ μm , quite thin (less than 0.5 μm in thickness). Not certainly proper as they are not visible in the sections.

Distribution and ecology. Red Sea, Aqaba, under overhangs in reef localities.

Etymology. Named after Dr Oliver Voigt, München, for his excellent contributions to Calcarea systematics.

Remarks. The present specimen resembles to some extent Voigt *et al.*'s (2017) description of *Borojevia* aff.

aspina (Klautau *et al.*, 1994). The trichoxea-like spicules are present in the spicule slide at a low frequency. In the surface section (Fig. 6c) there are some thin long spicules, but they are indistinct and may not be proper to the sponge. Voigt *et al.* also observed that the trichoxeas are difficult to find in the slides. Voigt *et al.* did not observe spines on the apical actines of the tetractines, which is a distinct difference. In our new species the spines were very small and occasionally absent in our specimen (Figs 7c left), thus we assume our and Voigt *et al.*'s specimens belong to different closely related species. Like Voigt *et al.*'s specimen ours has whitish color and it lacks distinct tripods. Since *Borojevia aspin*a is a Brazilian species, the likelihood that a species living on reefs in the Red Sea is conspecific with the Brazilian population is judged to be quite small.

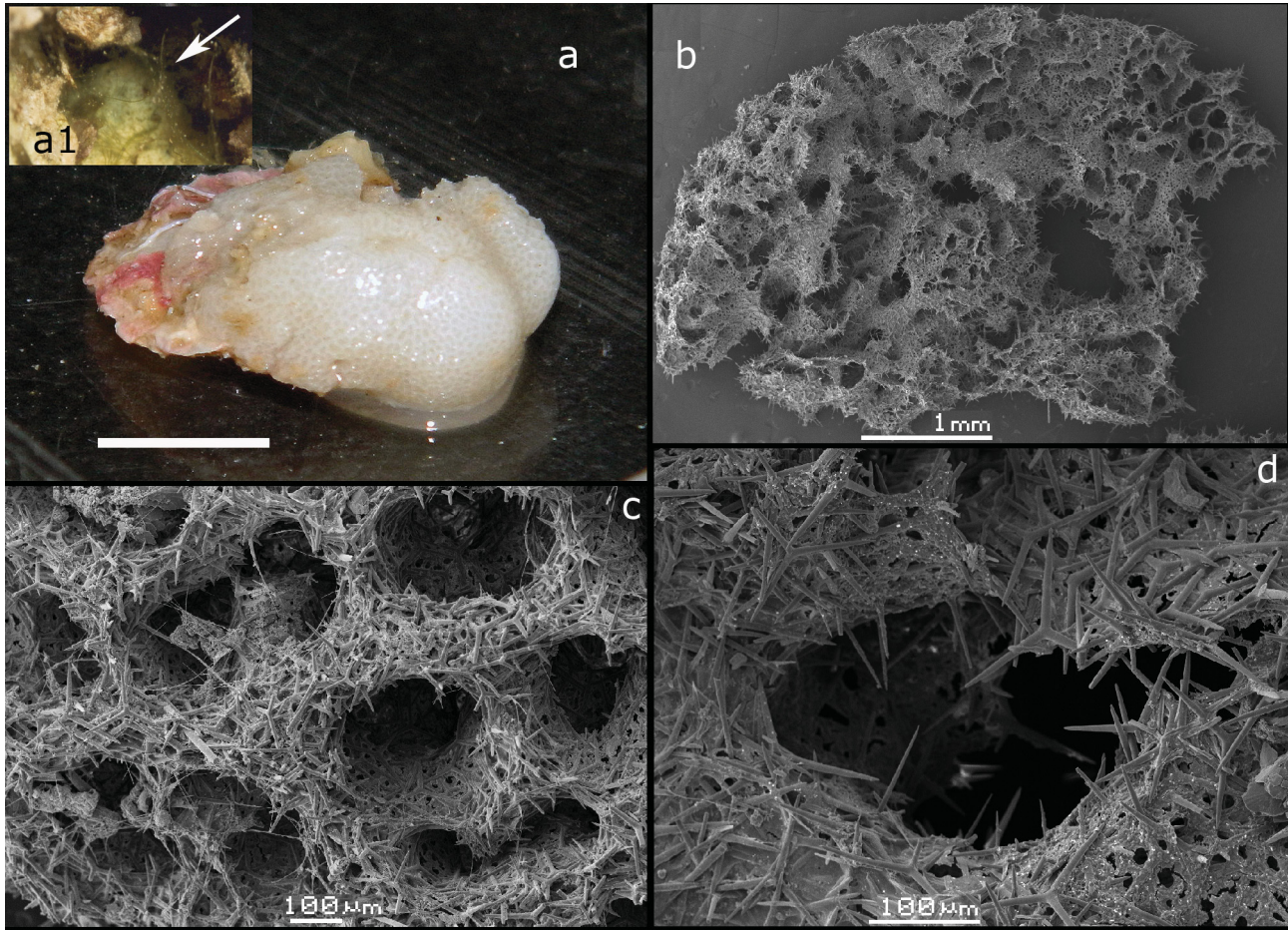


FIGURE 6. *Borojevia voighti* sp. nov., holotype ZMA Por. 13444, a, preserved holotype (scale bar = 1 cm), a1, small indistinct in situ image of holotype (arrow) growing in a hollow of a pillar in the Eilat container harbor, Israel (photo cut out from larger image made by M. Wunsch), b–d, SEM images of sections of the holotype, b, cross section, c, surface section, d, enlarged part of cross section showing protruding apical actines of tetractines.

Borojević (1967) described the Mediterranean species *Clathrina cerebrum* from Eastern South Africa (Natal coast). This combination is now assigned to *Borojevia* and restricted to the Mediterranean (cf. Klautau *et al.* 2016). It is cushion-shaped like the new species, but it has tripods, making it unlikely to be the same species.

So far, no other species of *Borojevia* have been reported from the region, but below we will describe two additional species. Differences with the present species will be given in the Remarks sections of these species.

We were unable to obtain a partial 28S rRNA sequence of this specimen.

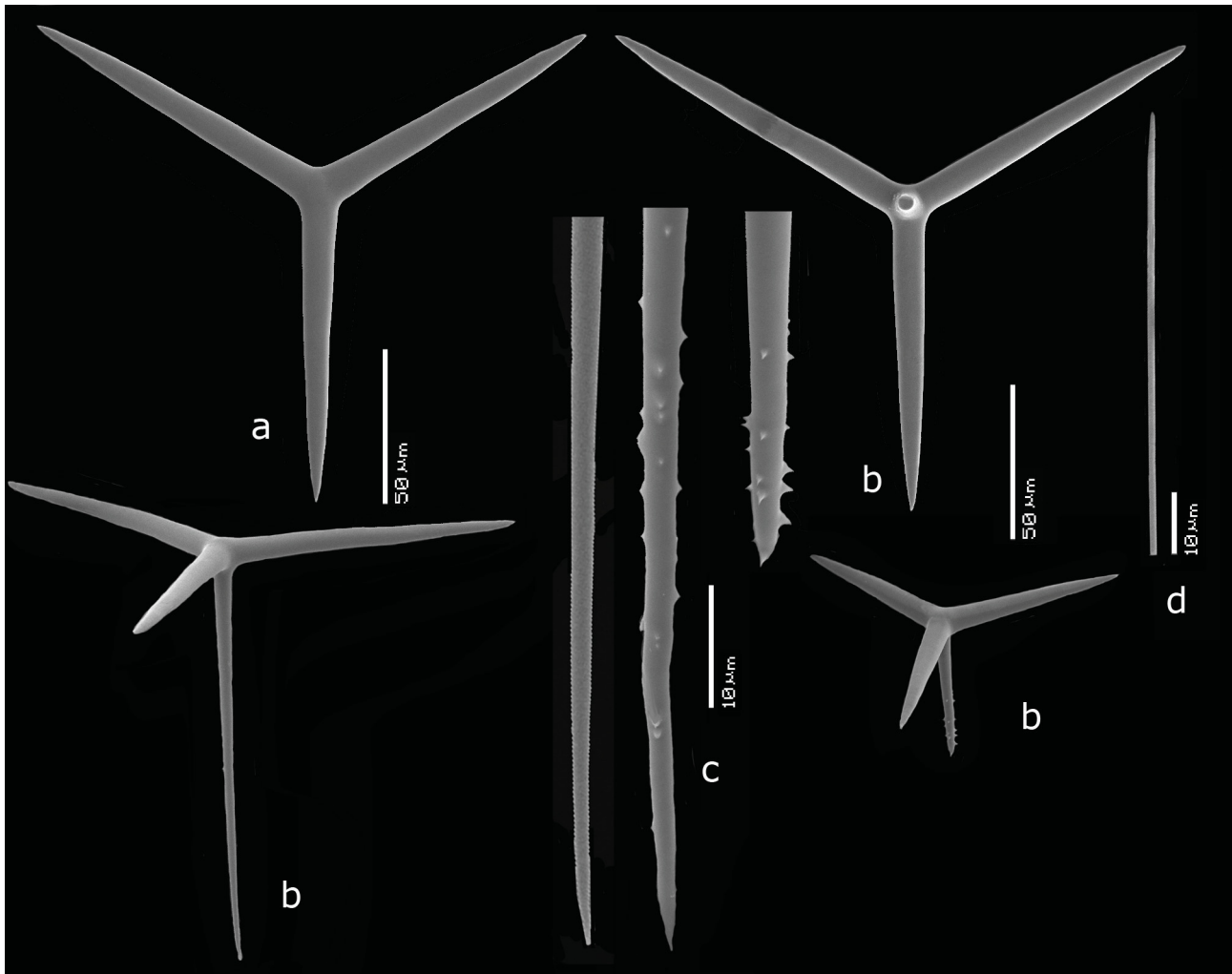


FIGURE 7. *Borojevia voighti* sp.nov., holotype ZMA Por. 13444, SEM images of spicules, a, triactine, b, tetractines, c, details of apical actines of tetractines showing entirely smooth, vestigial spined, and clearly spined conditions, d, fragment of assumed trichoxea.

***Borojevia tubulata* sp.nov.**

Figures 8a–c, 9a–f, 10a–h, 11a–f

Material examined. Holotype, RMNH Por. 10158, Maldives, Faafu Atoll, Wallstreet, 3.119°N 72.979556°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. MAD10/MAS119, 20 February 2015.

Paratype, RMNH Por. 10113, Maldives, Faafu Atoll, Free Climbing, 3.066583°N 72.923028°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. MAD06/MAS068, 18 February 2015.

Additional material, ZMA Por. 12435, Seychelles, Amirantes, Desroches Atoll, SW rim, outer reef slope, 5.7167°S 53.6167°E, depth 5–30 m, scuba, coll. M.J. de Kluijver, NIOP-E stat.nr. 774/04, 30 December 1992.

Description. Irregularly arranged, groups of tubular individuals, the walls of which consist of tightly anastomosed tubuli. In situ white (Figs 8a, 10a) or cream or yellow-white (Fig. 8b) colored, on deck (Figs 8c, 10b) and preserved they are cream to pale beige (Figs 10c, 11a). Height of tubes up to about 3 cm, width 0.5 cm at the aperture and 1 cm at the base, but individual tubes may be smaller and thinner. Tube apertures are about as wide as the (pseudo-)atrium or slightly narrower. In preservation the tubes collapse to form easily damaged soft and flabby fragments (Figs 8c, 10b–c, 11a), which have their (pseudo-)atrium flattened to a narrow slit (Fig. 11b). The tube walls are ‘punctate’ (Figs 9a, 10d) caused by regularly distributed pseudopores (cf. Dendy’s (1913) description of *Ascaltis gardineri*, as *Leucosolenia*), which give access to the densely crowded tubuli.

Aquiferous system. Asconoid.



FIGURE 8. *Borojevia tubulata* sp.nov., holotype RMNH Por. 10158, from the Maldives, a, habitus of one of the groups of tubes white-colored, b, ditto cream-colored (both sampled groups of tubes were included in a single preserved sample and were subsequently not separated and were together joined as the holotype), c, holotype photographed on deck after collection (scale bar mm) (photographs N.J. de Voogd).

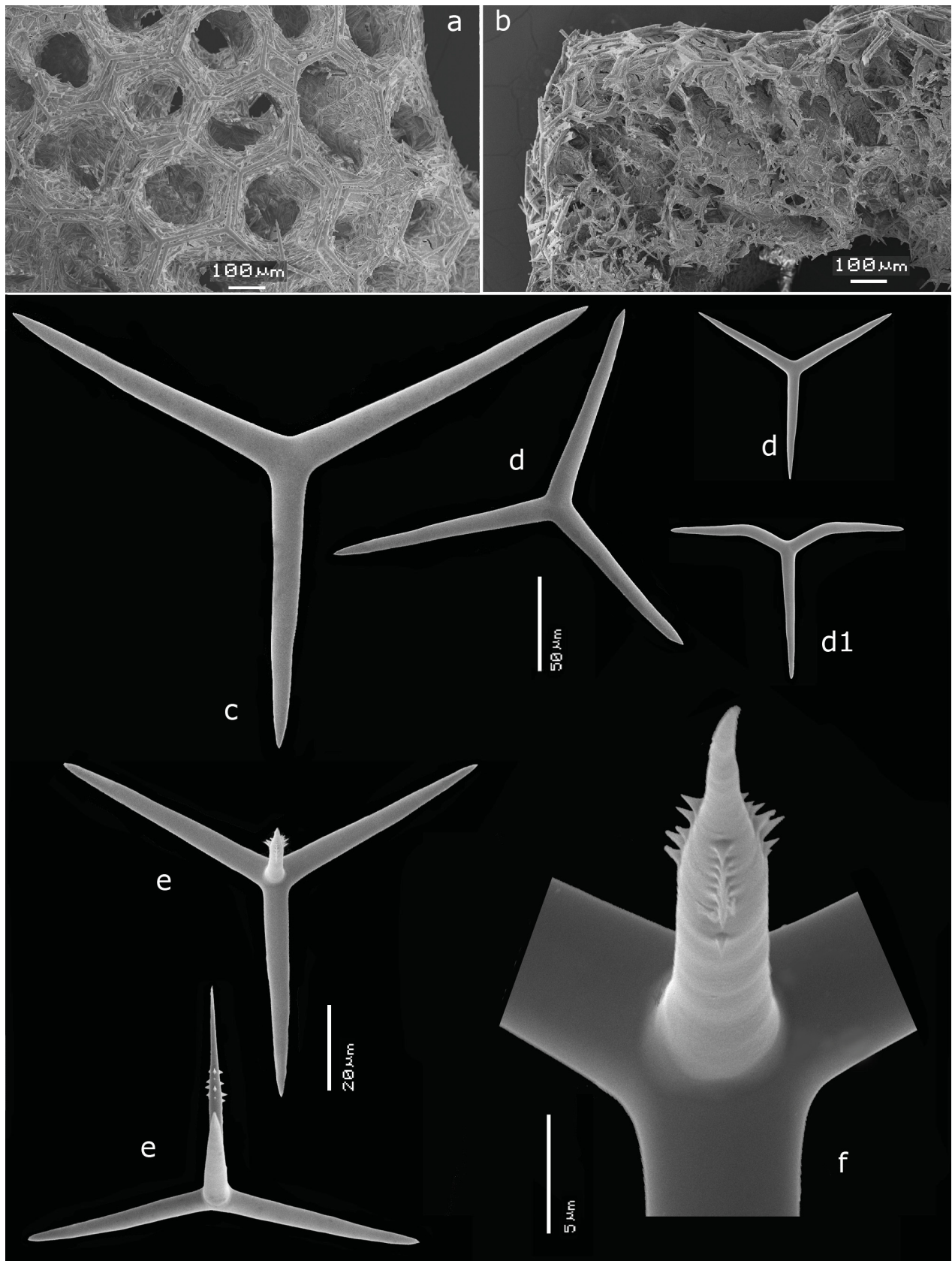


FIGURE 9. *Borojevia tubulata* sp.nov., holotype RMNH Por. 10158, from the Maldives, SEM images of sections and spicules, a, view of surface showing pseudopores and large triactines at the surface, b, cross section of tube wall, upper part outside, lower part pseudoatrium, c–f, SEM images of the spicules, c, large triactines from the outer surface, d, smaller triactines from the inner tubuli, d1, sagittal triactine, e, tetractines, f, detail of spined apical actine of tetractine. Please note that rows of spines are in line with the basal radiate system.

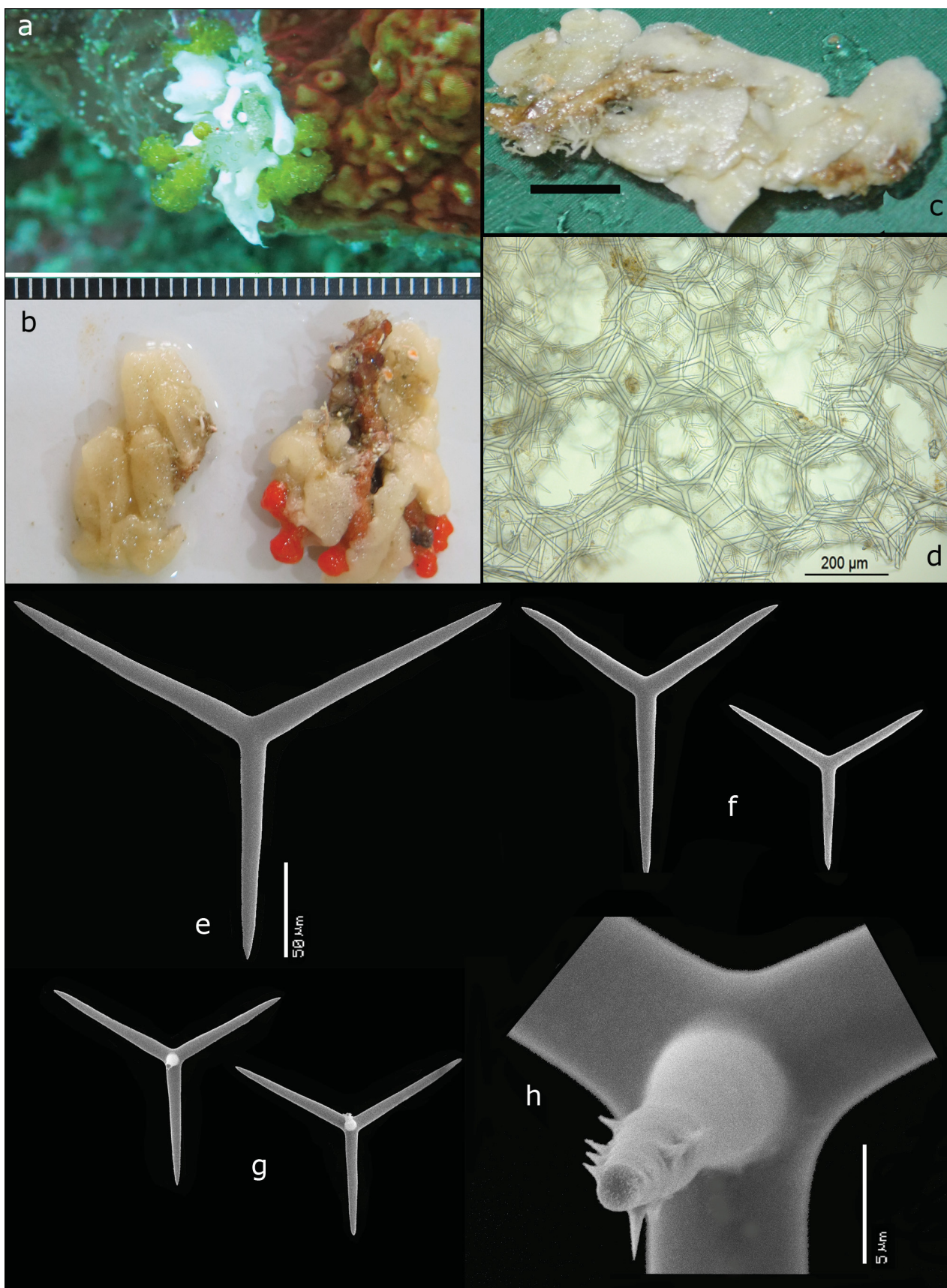


FIGURE 10. *Borojevia tubulata* **sp. nov.**, paratype RMNH Por. 10113, from the Maldives, a, in situ white group of tubes (photo N.J. de Voogd), b, on deck fragmented groups of tubes (scale bar mm), c, preserved paratype (scale bar = 1 cm), d, light microscopic image of surface skeleton showing characteristic pattern of larger triactines, e–h, SEM images of spicules, e, large triactine of the outer surface, f, small triactines of the inner tubuli, g, tetractines, h, detail of spined apical actine of tetractine.

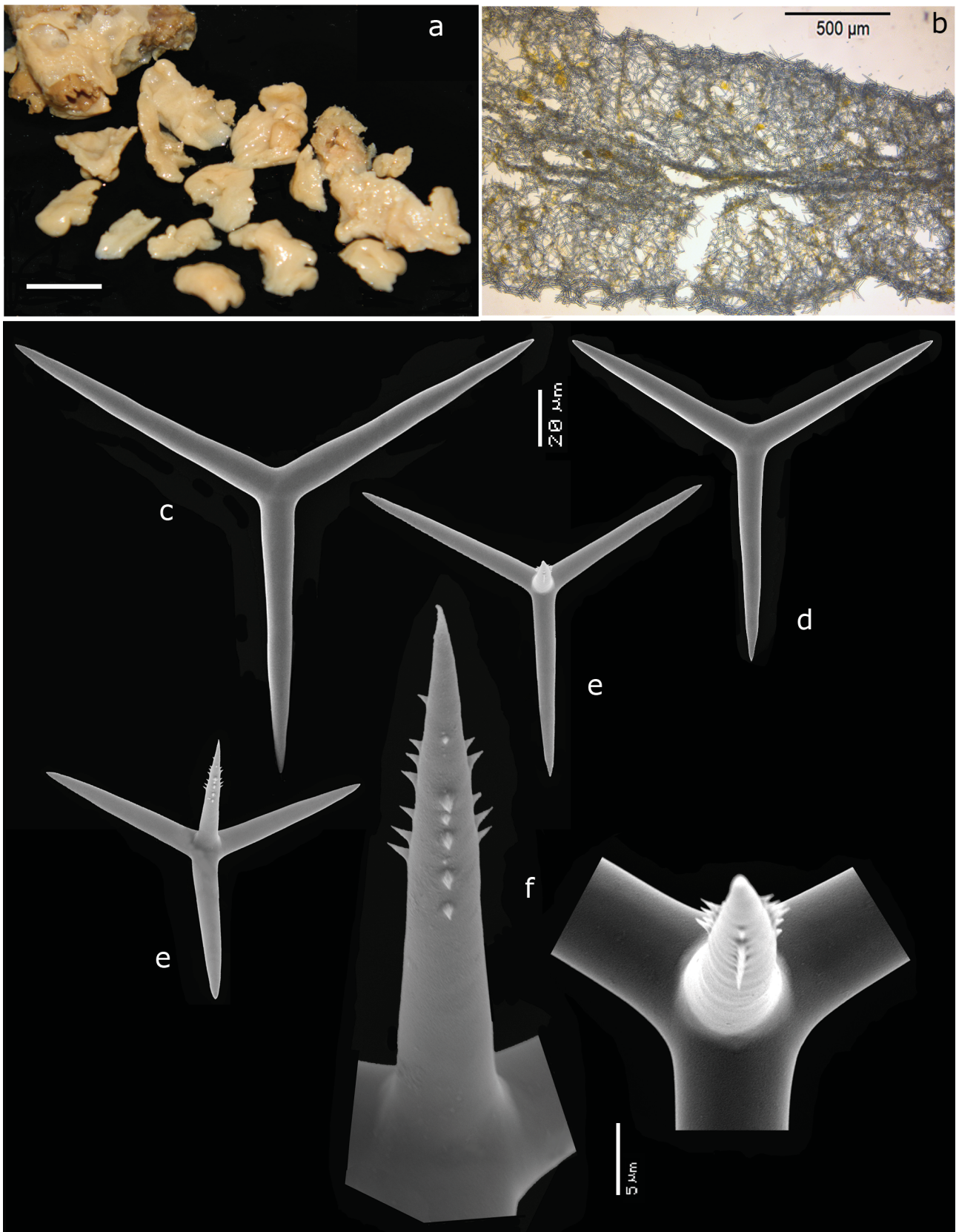


FIGURE 11. *Borojevia tubulata* **sp.nov.**, ZMA Por. 12435, from the Seychelles (Amirantes region), a, preserved habitus of fragmented tubes (scale bar = 1 cm), b, cross section of flattened tube with slit-like flattened pseudoatrium, c–f, SEM images of spicules, c, large triactine of the surface, d, small triactine of the interior skeleton, e, tetractines, f, details of spined apical actines of the tetractines.

Skeleton. The pseudopores of the outer tube walls are strengthened by larger triactines, arranged in a distinct cortical pattern (Figs 9a, 10d), the skeleton of the walls of the tubuli are built by one-two layers of smaller triactines and tetractines, with the apical actines of the tetractines protruding into the lumina of the tubuli. The atrial sides of the tube walls (Fig. 9b) have an irregular skeleton and do not exhibit a special arrangement of larger triactines as observed on the outer wall, which indicates that the atrium is in fact a pseudoatrium, as is characteristic of the genus *Ascaltis* according to the Systema Porifera (Borojević *et al.* 2002a). See below for a further discussion.

Spicules. (Figs 9d–f, 10e–h, 11c–f) Triactines in two size classes, tetractines with spined apical actines. The latter invariably have the spines in three distinct rows the position of which match the basal triadial system. We did not observe the presence of tripods, but we presume the larger category of triactines is homologous. Because of slight discrepancies between the specimens, we provide separate images of the samples and measurements of the three samples:

Holotype RMNH Por. 10158: Larger triactines (Fig. 9c) of the outer tube wall, equiradial or very rarely sagittal, robust, with conical actines, which may slightly differ in length in the same spicule, actines 92–133–189 x 11–13.4–16 µm.

Smaller triactines (Figs 9d,d1), equiradial (Figs 8d), or rarely sagittal (Fig. 9d1) with undulate paired actines, measuring 54–63–111 x 5–6.3–7.5 µm.

Tetractines (Figs 9e–f), with basal triradial system usually equiradial, but very occasionally there may be sagittal spicules, 51–68–96 x 6–6.6–9 µm, apical actines (Fig. 9f) 24–37–48 x 3.5–4.4–5 µm.

Paratype RMNH Por. 10113: Larger triactines (Fig. 10e) with conical actines, 129–151–174 x 14–15.2–18 µm; one single sagittal triactine was observed in the slides.

Smaller triactines (Figs 10f), with conical actines, 59–72–93 x 6–7.2–10 µm.

Tetractines (Figs 10g), with conical actines, those of the basal radial system 48–67–78 x 4.5–6.6–8 µm, apical actines with spines (Fig. 10h), 35–43–58 x 4–5.2–7 µm.

ZMA Por. 12435 (Figs 11c–f): Larger triactines (Fig. 11c), 102–117.6–134 x 11–13.4–17 µm

Smaller triactines (Fig. 11d), 51–75.1–94 x 6–8.4–10 µm

Tetractines (Figs 11e), 61–76.3–88 x 7–8.6–10 µm, apical actines with spines (Figs 10f), 40–53.4–74 x 6–6.6–7 µm.

Distribution and ecology. Maldives, Seychelles, under overhangs on coral reefs, depth 5–30 m.

Etymology. *Tubulatus* (L.) means tube-shaped, referring to the habitus of the species.

Remarks. The three samples show some discrepancies, which we consider to be infraspecific variability. The two Maldives samples have similar habitus, but show some color differentiation between distinctly white and more creamy or pale yellow. The holotype has a larger proportion (though still a clear minority) of sagittal tri- and tetractines than the paratype. The Seychelles specimen was noted to be yellow in color, and it lacks sagittal spicules entirely. The Seychelles specimen has smaller triactines than the Maldives and the distinction between larger and smaller spicules is less obvious. For this reason, we limited the type material to that of the Maldives only. However, we believe that the three samples are conspecific.

The species is assigned to the genus *Borojevia* despite the elaborate shape and presence of a pseudoatrium, and despite the absence of clear tripods among the triactines. In fact, we initially assigned the specimens to the genus *Ascaltis*, based on the habitus and skeletal structure and because a Western Indian Ocean species, *Ascaltis gardineri* (Dendy, 1913) appeared to be close in skeletal characters. The major difference between that species and our specimens is the lobate, non-tubular habitus in the former.

Molecular sequence data (partial 28S, cf. Fig. 2B) were obtained for the holotype and the Seychelles material of *Borojevia tubulata* **sp.nov.** Our phylogenetic analysis of Calcinean sequences, obtained from our own Western Indian Ocean samples, Voigt *et al.*'s (2017) samples (we were allowed to include a recent sequence of *Borojevia* sp. from the Maldives kindly sent to us by Oliver Voigt, which is likely a member of the present new species), and from GenBank, clearly showed that the present species is closely related to *Borojevia aspina* (Klautau *et al.*, 1994), *Borojevia* aff. *aspina* sensu Voigt *et al.* 2017, *B. cerebrum* (Haeckel, 1872), *B. brasiliensis* (Solé-Cava *et al.* 1991) and a new *Borojevia* species described below, and was distant from *Ascaltis reticulum* (Schmidt, 1862), the only *Ascaltis* for which molecular data are available. As Klautau *et al.* (2016) pointed out, we cannot be certain about the molecular affiliation of the genus *Ascaltis* yet, because there are no sequences available for the type species *Ascaltis lamarki* (Haeckel, 1872). We have chosen to follow the molecular signal and keep our species in the genus *Borojevia*, against the weight of morphological evidence for a possible membership of *Ascaltis*.

The new species differs from the above-described *Borojevia voighti* **sp.nov.** in the presence of a pseudoatrium and the more prominent and consistent spination of the apical actines of the tetractines.

A further similar species appears to be *Leucascus simplex* Dendy, 1892, from South Australia, reported also from Providence Island in the Seychelles by Dendy (1913). The type of that species has spined apical actines (cf. redescription of *L. simplex* in Cavalcanti *et al.* 2013), but it has not been verified for the Providence specimen. This differs from the present species also in habitus (massive, with only a slit-like atrial cavity). Below we describe a new species of *Leucascus* from Eastern South Africa. Apart from a more elaborate shape, it is distinct by having a surface palisade of short diactines. The present species is not a likely *Leucascus*, as in our phylogeny of Fig. 2, *Leucascus flavus* Cavalcanti *et al.*, 2009 is not at all closely related to *Borojevia* species.

***Borojevia pirella* sp.nov.**

Figures 12a–b, 13a–e

Material examined. Holotype, RMNH Por. 11622a, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG023, 16 October 2016.

Paratype, RMNH Por. 11622b, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG023, 16 October 2016.

Description. Small pear-shaped cormus (Figs 12a–b) consisting of a mass of moderately tightly anastomosed tubuli separated by rounded or polyangular spaces. Color white, semitransparent. Size approximately 1.5 cm high, 1 cm in diameter. Tubuli approximately 0.2 mm in diameter. The narrow end is provided with an oscule of about 2 mm diameter, leading into a short water-collecting tube and a pseudoatrium. Preserved material consists of two specimens (Figs 12a1, holotype, and 12b1, paratype), which collapsed to form flattened objects with soft consistency.

Aquiferous system. Asconoid.

Skeleton. The pseudoatrium has no special skeleton, it is merely a space between the anastomosed tubuli (Fig. 13a). The wall of these is thin, having one or two spicules comprising a mixture of triactines and tetractines, the latter with the apical actines protruding into the lumen of the tubuli.

Spicules. (Figs 13b–e) Triactines and tetractines of approximately the same size, no differentiated larger and smaller triactines are present.

Triactines (Fig. 13b–c) equiangular and equiradiate (Fig. 13b), with a tendency to become slightly sagittal, with a longer unpaired actine; occasionally triactines are irregular with one of the actines wavy and distinctly sagittal (Fig. 13c). Actine dimensions 51–81.3–93 x 5–6.7–8 µm.

Tetractines (Fig. 13d–e), similar in size and shape to the triactines (Figs 13d), with apical actines provided with three prominent conical spines in one verticil the position of which is matching the basal triradiate system (Figs 13e). Actines of the basal triad system 72–85.7–96 x 5.5–7.1–8 µm, apical actines 31–58.4–76 x 5–5.9–7 µm.

Distribution and ecology. Rodrigues, Mascarene Islands, on coral reefs at 12 m depth.

Etymology. Pirella (L.), a feminine noun, meaning a small pear, referring to the habitus of the sponge.

Remarks. Despite the presence of a pseudoatrium and spined apical actines of the tetractines, molecular sequence data indicate clearly (Fig. 2B) that this species is closely related to *Borojevia* aff. *cerebrum* and ‘*Ascaltis* OV-2012’, both reassigned to *Borojevia* (cf. Klautau *et al.* 2016), and not to *Ascaltis reticulum*. Voigt *et al.*’s (2012) Australian species ‘*Ascaltis* OV 2012’ has a clear pseudoatrium illustrated in their Supporting Fig. S1 inset J, but its sequence is grouped unequivocally among the *Borojevia*’s in our Fig. 2B phylogeny. This justifies assignment of the present species to the genus *Borojevia*. The triactine complement of *B. pirella* **sp.nov.** does not contain any clear tripods, as is one of the additional features described for the genus *Borojevia*. The presence of the pseudoatrium is shared with the above described *B. tubulata* **sp.nov.**, but apparently is absent in *B. voighti* **sp.nov.** and other *Borojevia* spp. The relationship with *Ascaltis* remains unresolved. The three prominent spines on the apical actines of the tetractines are a special feature of the new species. It is shared with the recently described Brazilian *Borojevia trispinata* Azevedo *et al.*, 2017. This is generally similar in spicule sizes, but on average has slightly smaller actines. The habitus differs in lacking a central pseudoatrium and being more irregular in shape, not pear-shaped.

We obtained sequences for *Borojevia tubulata* **sp.nov.** (both holotype and non-type Seychelles specimen, cf.

above) and *Borojevia pirella* **sp.nov.** (both holotype and paratype). We compared these with two sequences of Red Sea specimens of *Borojevia* aff. *aspina* provided by Oliver Voigt in a separate restricted phylogenetic analysis. The aligned and trimmed sequences (length 426 sites) revealed that both identical sequences of *B. pirella* **sp.nov.** showed 4–5 sites difference with *B. aff. aspina* sensu Voigt *et al.* 2017, 12–22 sites difference with *B. tubulata* **sp.nov.** (the higher difference being with the Seychelles specimen, as the holotype and Voigt's *Borojevia* sp. have identical sequences). It may be concluded that the new species and *Borojevia* aff. *aspina* are more closely related than each of them with *B. tubulata* **sp.nov.**

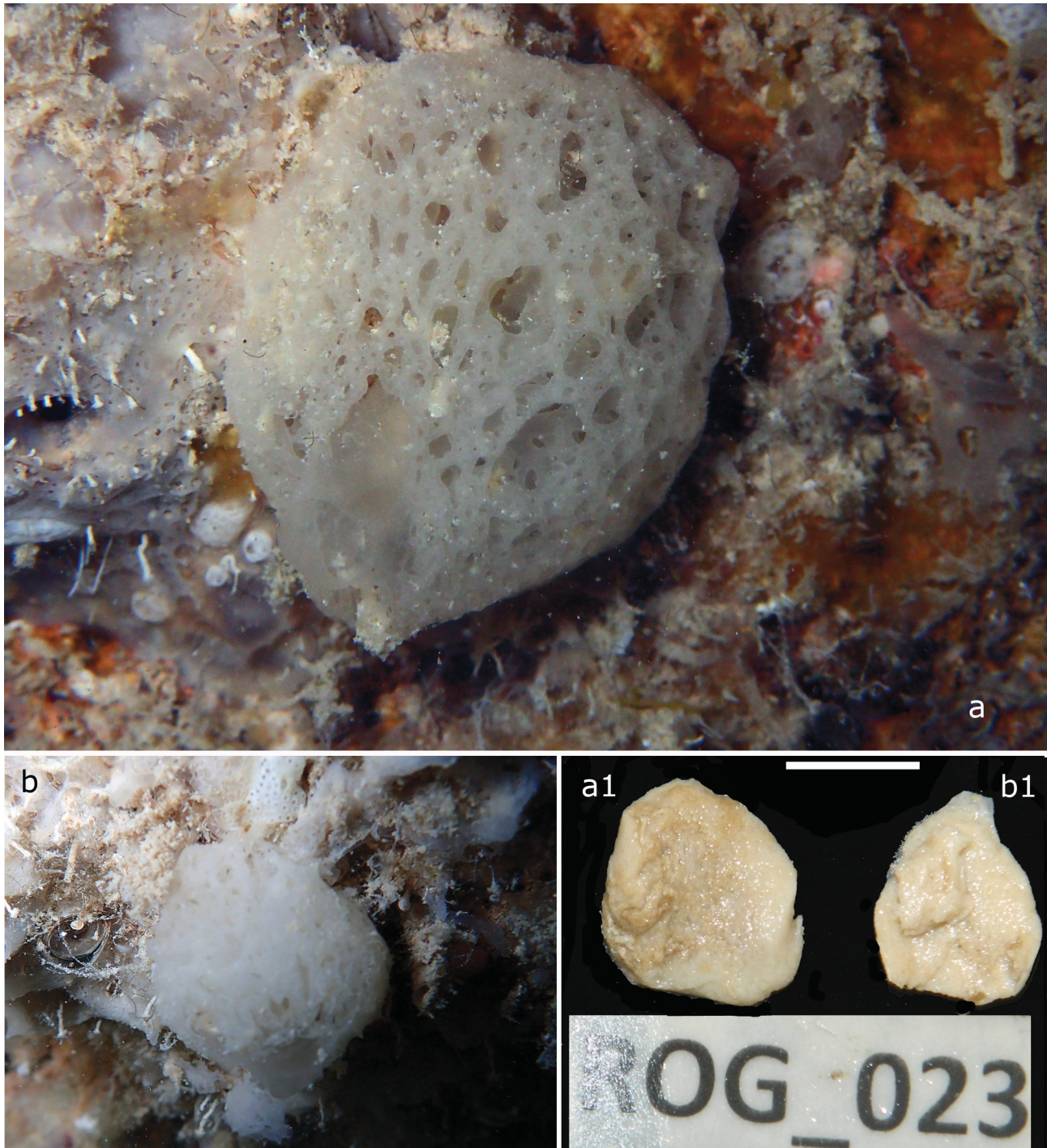


FIGURE 12. *Borojevia pirella* **sp.nov.**, a, habitus in situ of holotype RMNH Por. 11622, from Rodrigues, the easternmost of the Mascarene Islands (photo N.J. de Voogd), a1, preserved holotype (scale bar = 1 cm), b, habitus in situ of paratype RMNH Por. 11622b (photo N.J. de Voogd), b1, preserved paratype.

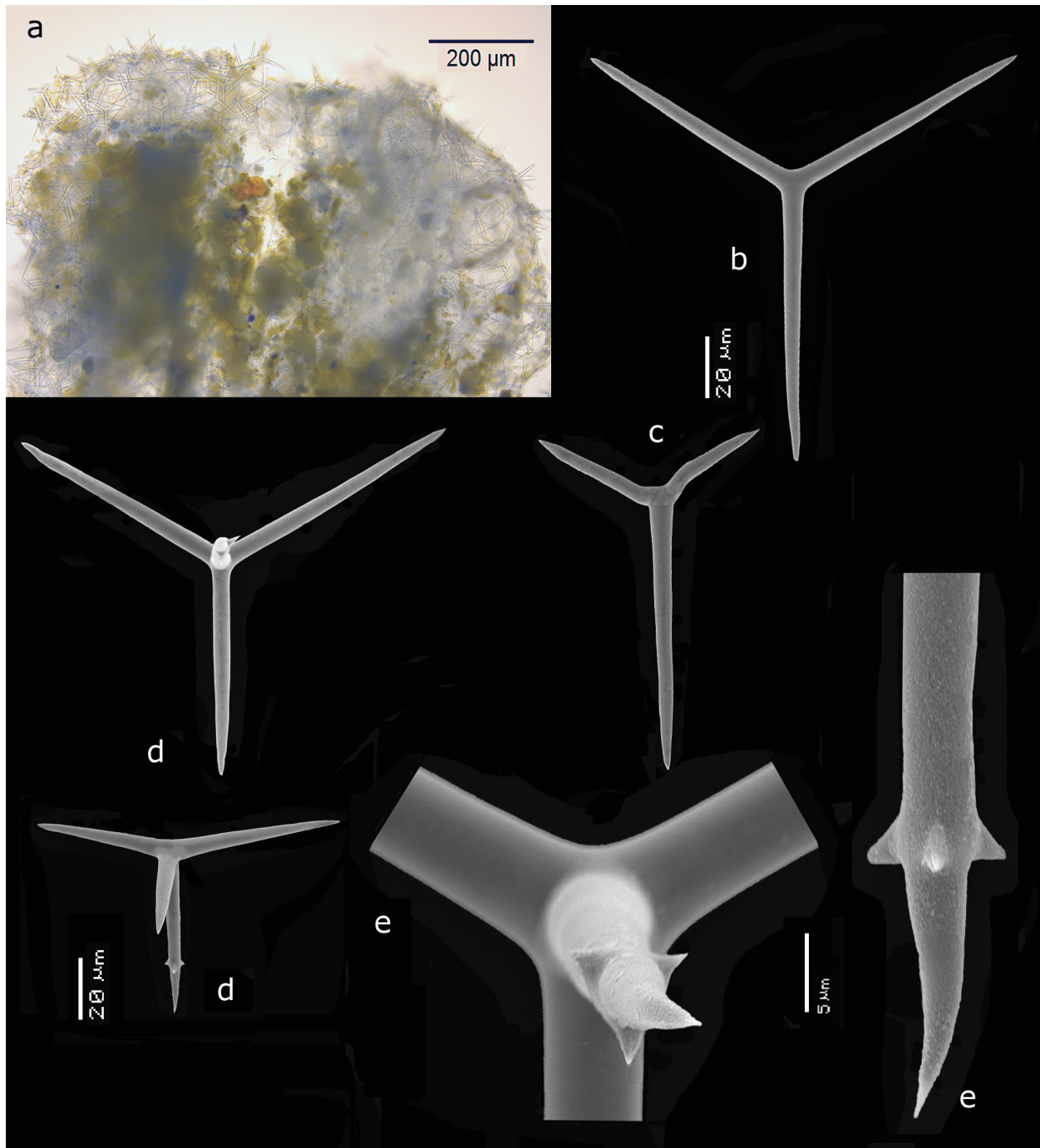


FIGURE 13. *Borojevia pirella* **sp.nov.**, holotype RMNH Por. 11622, from Rodrigues, a, light microscopic cross section of oscular region showing pseudoatrium and surrounding tubuli, b–e, SEM images of the spicules, b, regular triactine, c, rare sagittal irregular triactine, d, tetractines, e, details of apical actines of the tetractines showing characteristic verticil of three conical spines.

Molecular comparison of *B. pirella* **sp.nov.** with the similar Brazilian species *B. trispinata* is complicated by differences in the target genes (our 28S vs Azevedo *et al.* 2017's ITS). In a special effort, we obtained additional ITS data for *B. pirella* **sp.nov.** and aligned two ITS sequences (holotype and paratype, which appeared to be identical, not submitted to GenBank) with two sequences of *B. trispinata* downloaded from GenBank (UFRJPOR6419 and 6487, showing several site differences). A trimmed 792 sites alignment of the four sequences shows considerable differences (25 non-conserved sites differed between the two species, not counting a gap of 27 sites). Nevertheless, the morphological resemblance of the two species from the Western Indian Ocean and the Western Atlantic Ocean region is striking.

Genus *Clathrina* Gray, 1867 sensu Klautau *et al.* 2013

Remarks. The species of the former large genus *Clathrina* have been subdivided by Klautau *et al.* 2013 into distinct genera. The restricted genus *Clathrina* unites the species with asconoid tubuli anastomosed into loosely organized or more tightly anastomosed cormi with spiculation consisting exclusively of small triactines. We obtained a considerable number of partial 28SrRNA sequences to assist us in classifying the collected members of this still very large genus. We combined our sequences with our Indonesian, Oliver Voigt's (2017), Sponge Barcode Project and GenBank *Clathrina* sequences in an analysis the results of which are given in the phylogenetic tree of Fig. 2A. See above for further comments on the results.

Clathrina sinusarabica Klautau & Valentine, 2003

Figures 14a–d, 15a–d

Clathrina coriacea; Row 1909: 184 (not: Montagu 1814).

Clathrina sinusarabica Klautau & Valentine, 2003: 45, fig. 37; Voigt *et al.* 2017: 12, fig. 7.

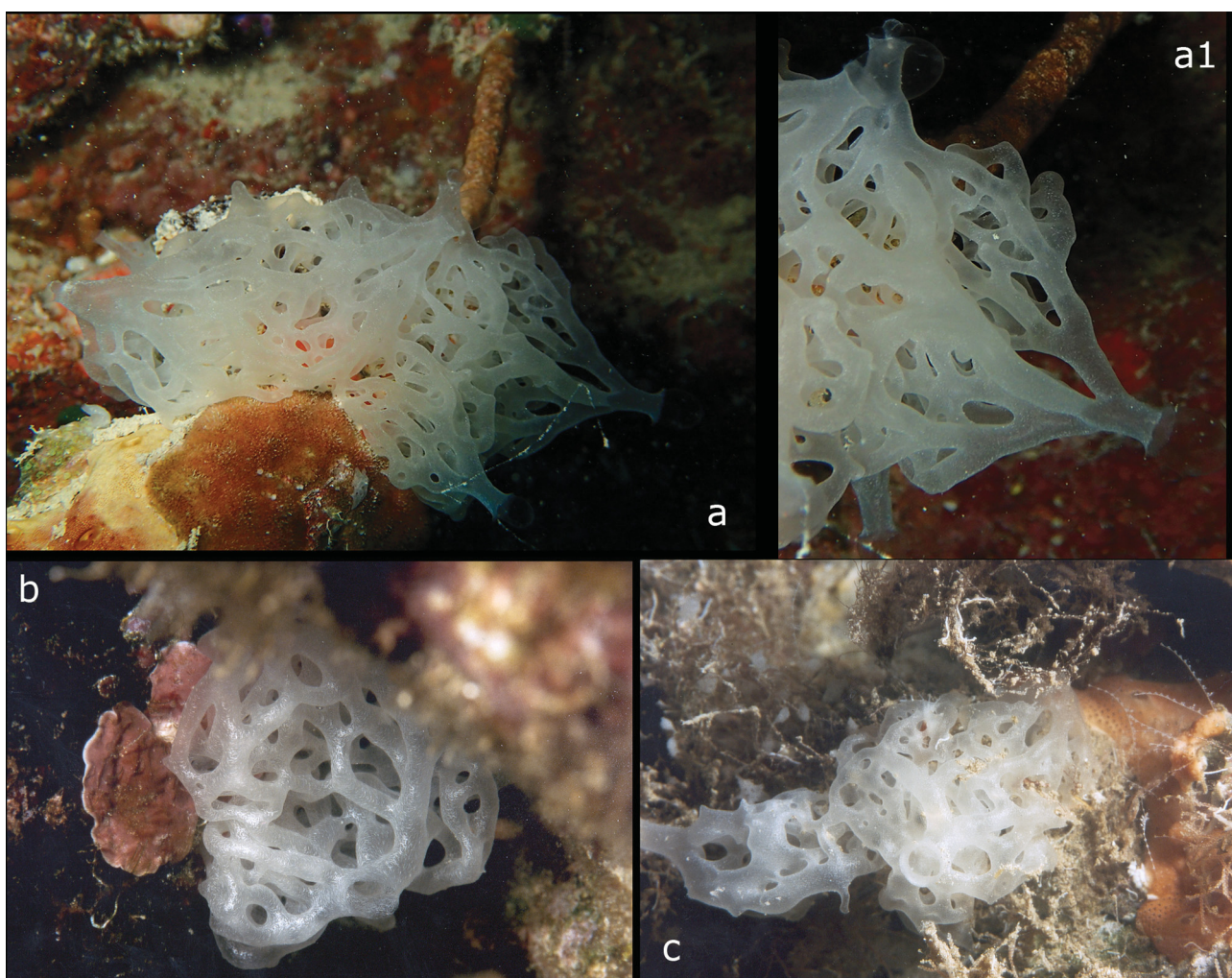


FIGURE 14. *Clathrina sinusarabica* Klautau & Valentine, 2003, a, RMNH Por. 10003, from the Saudi Arabian Red Sea, Jeddah (field nr. JED210), in situ on the reefs of Jeddah, a1, detailed view of water collecting tubes of the same (photos N.J. de Voogd), b, ZMA Por. 13414, at Aqaba, in situ on Schuhmacher's Pinnacle, c, ZMA Por. 13476, at Aqaba's container port (photos M. Wunsch).

Material examined. RMNH Por. 10003, Saudi Arabia, Jeddah, near Thuwal, Tahlah, 22.25725°N 38.880917°E, scuba, coll. N.J. de Voogd, field nr. THU14/JED 210, 13 November 2014; ZMA Por. 13414, Israel, Schuhmacher's

Pinnacle, Gulf of Aqaba, depth 6 m, scuba, coll. M. Wunsch, field nr. AQ11, 1 July 1998; ZMA Por. 13476, Israel, pillar container port, Gulf of Aqaba, depth 5 m, scuba, coll. M. Wunsch, field nr. AQ61, 5 July 1998.

Description. Cushion of loosely anastomosed semi-transparent white tubuli (Figs 14a–c) of 0.5–1.2 mm diameter. Water collecting tubes (Fig. 14a1) are common at the upper and lateral sides, but are less prominent in the Aqaba specimens (Figs 14b–c). Preserved material is now fragmented and has pinkish color in alcohol. Size of the entire Jeddah specimen is 5 x 3 x 2 cm, the Aqaba specimens are slightly smaller.

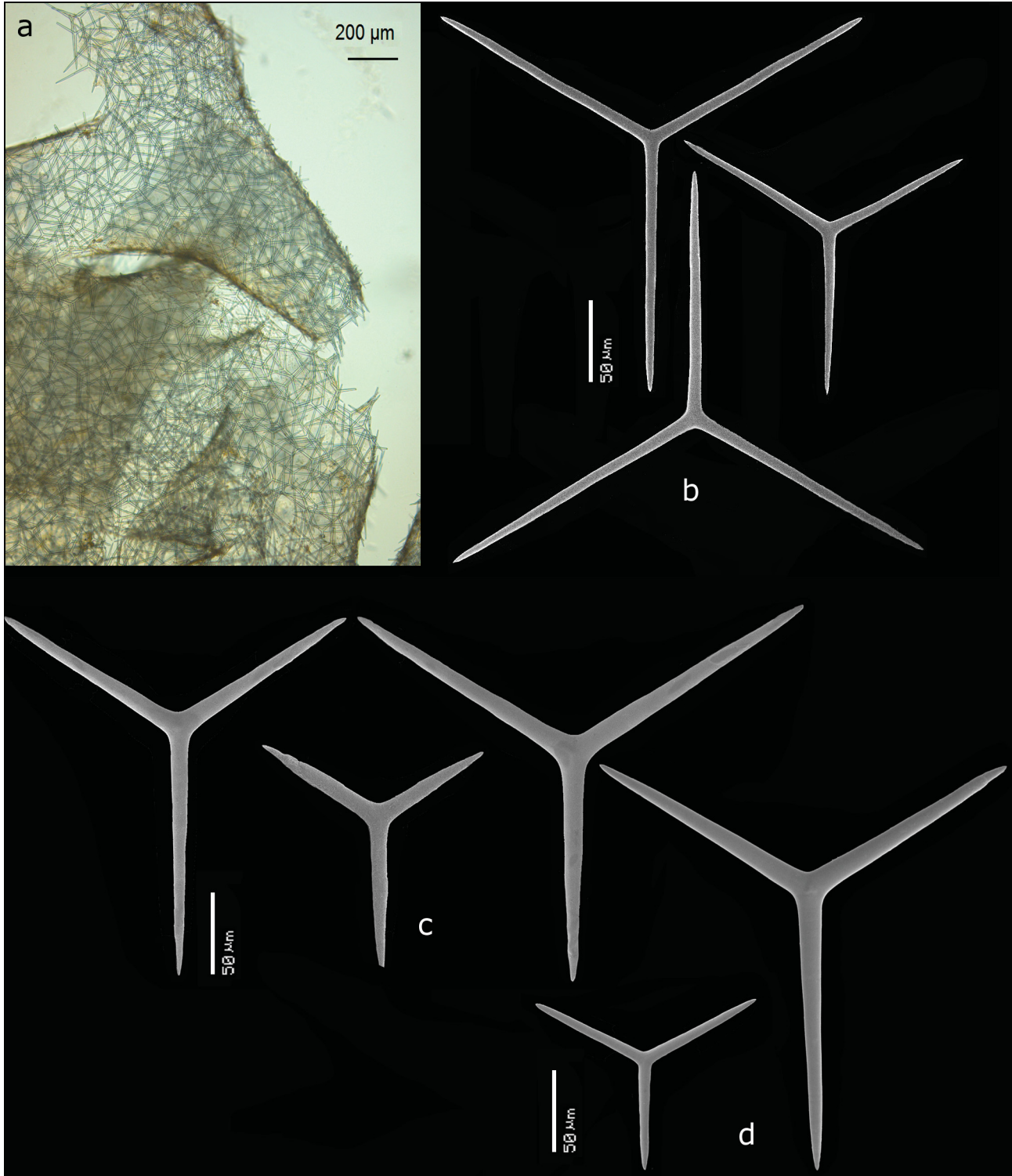


FIGURE 15. *Clathrina sinusarabica* Klautau & Valentine, 2003, a, light microscopic view of part of the cormus and tubuli of RMNH Por. 10003 from Jeddah, b–d, SEM images of spicules, b, of Jeddah specimen RMNH Por. 10003, c, of Aqaba specimen ZMA Por. 13414, d, of Aqaba specimen ZMA Por. 13476.

Aquiferous system. Asconoid.

Skeleton. (Fig. 15a) Tubule walls thin, with single layer of spicules.

Spicules. (Figs 15b–d) Equiradial equiangular triactines with thin cylindroconical actines ending in pointed apices, 78–214 x 7.5–17.5 μm (n=75).

The spicules sizes of the three specimens are:

RMNH Por. 10003: 83–164.4–194 x 7.5–9.04–11 μm

ZMA Por. 13414: 107–167–214 x 9–13.4–17.5 μm

ZMA Por. 13476: 78–132–162 x 9–11.2–14.5 μm .

Distribution and ecology. Saudi Arabia, Jeddah, on reefs; if correctly identified it occurs in the Sudanese Red Sea, Agig, and the Israelian part of the Gulf of Aqaba, on reefs, depth 5–6 m.

Remarks. The type of *Clathrina sinusarabica* Klautau & Valentine, 2003 resembles our specimens in habitus and color, but the actines of its spicules are significantly shorter, 72–103 x 8.4 μm (according to Klautau & Valentine 2003). We base ourselves for the identification on Voigt *et al.*'s (2017) description, which gives actines of 50–166 x 8–18 μm . The partial 28S sequence obtained for the Jeddah specimen conforms to Voigt's molecular data (cf. Fig. 2A). The Jeddah specimen was sequenced, the Aqaba specimens were not. The Aqaba specimens appear to be morphologically similar, so we assume they are members of *C. sinusarabica*, but we gave separate measurements of the spicules of the three specimens, just in case.

Morphologically, the present specimens resemble Rodrigues and Seychelles material described below as *Clathrina rodriguesensis* **sp.nov.**, having firm whitish tubuli and robust triactines, but molecular data do not support this similarity (cf. Fig. 2A).

The present specimens show also considerable resemblance to the Indonesian species *Clathrina sororcula* Van Soest & De Voogd, 2015, which has loosely anastomosed semi-transparent white tubes, cylindrical triactines of the same average length. Differences are the presence of several water-collecting tubes (raised oscules, absent in *C. sororcula*) and the greater size of the actines of the spicules. No molecular sequence data for *C. sororcula* could be obtained.

Clathrina rowi Voigt *et al.*, 2017, *Clathrina luteoculcitella* Wörheide & Hooper, 1999 and *Clathrina chrysea* Borojević & Klautau, 2000 sensu Van Soest & De Voogd 2015 are closely related in a molecular sense (cf. Fig. 2A). The New Caledonian type material of the latter was yellow, but life color of the Indonesian material was unknown. The color in alcohol is transparent-white like the present specimen. Spicule sizes match reasonably (75–144 x 7–11 μm), but actines are more conical. *C. rowi* and *C. luteoculcitella* are treated below.

***Clathrina rowi* Voigt *et al.*, 2017**

Figures 16a–c, 17a–c

Clathrina rowi Voigt *et al.*, 2017: 14, fig. 8.

Material examined. RMNH Por. 10002, Saudi Arabia, Jeddah, near Thuwal, Tahlah, 22.25725°N 38.880917°E, scuba, coll. N.J. de Voogd, field nr. THU14/JED209, 13 November 2014; ZMA Por. 13446, Israel, Gulf of Aqaba, North Pinnacle, in cave, depth 9 m, scuba, coll. M. Wunsch, field nr. AQ52, 4 July 1998.

Description. The RMNH Por. 10002 specimen in situ (Fig. 16a) is an overall loose mass of intermediate-sized tubuli, provided with several water-collecting tubes ending in oscules. Cormus anastomosed in places to densely connected smaller tubes. Individual tubes 0.4–2 mm in diameter. Color pale beige to dirty white, semi-transparent. Preserved specimen massive due to compression of tubules during preservation and manipulation in transport, 4.5 x 3 cm in lateral expansion, about 1 cm thick, dirty white in color. The ZMA Por. 13446 specimen (Fig. 17a) from Aqaba is small. It has a conical, transparent-white cormus with faint purple tinge, consisting of loosely, occasionally more tightly, anastomosed tubules, leading to a prominent single water-collecting tube ending in a wide oscule.

Aquiferous system. Asconoid.

Skeleton. (Figs 16b, 17b) Tubuli walls with one to two spicule layers, rather dense in preserved condition.

Spicules. (Figs 16c, 17c) Triactines only, neither specimen contained clearly identifiable trichoxeas as reported for some specimens in the type series.

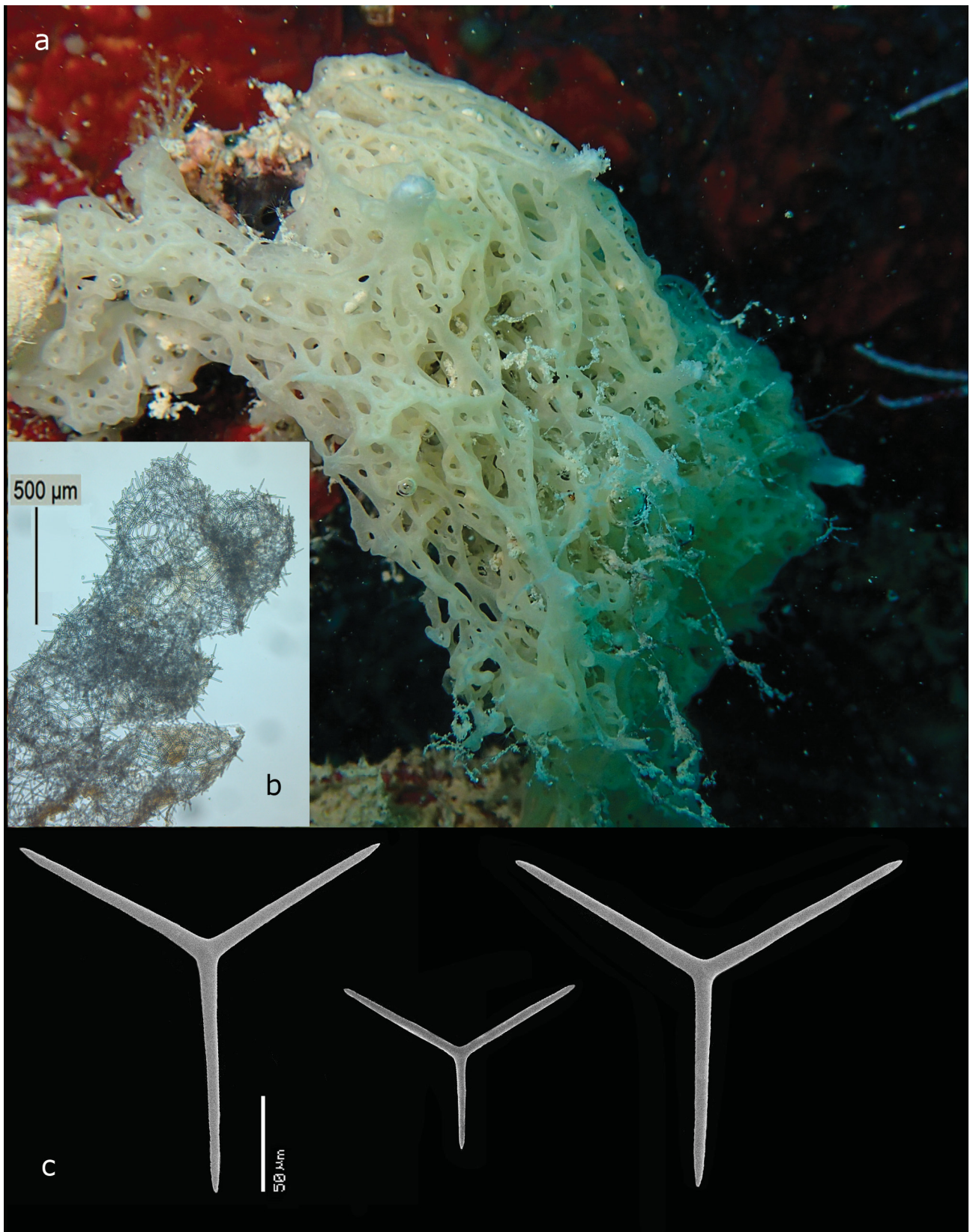


FIGURE 16. *Clathrina rowi* Voigt *et al.* 2017, RMNH Por. 10002, Saudi Red Sea, Jeddah, field nr. JED209, a, in situ on the reefs (photo N.J. de Voogd), b, light microscopic view of the cormus, c, SEM image of the spicules.

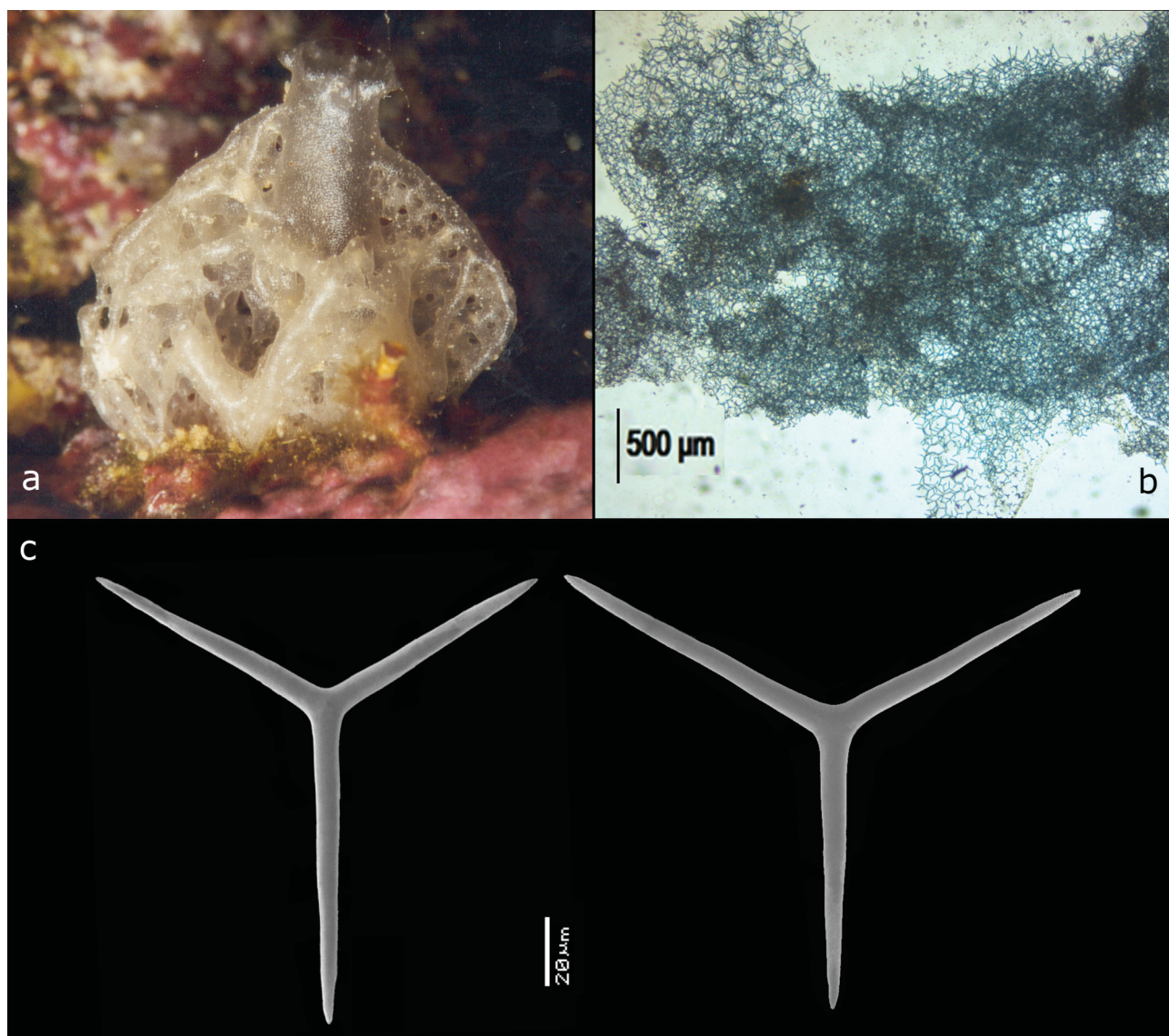


FIGURE 17. *Clathrina rowi* Voigt *et al.* 2017, ZMA Por. 13446, from Israel Red Sea, Aqaba, a, in situ in cave, b, light microscopic view of the cormus, c, SEM image of the spicules.

Triactines with thin cylindroconical actines, endings mucronate to shortly pointed, occasionally slightly sagittal, size range limited, in RMNH Por. 10002 it is 68–124–151 x 7.5–9.3–11 µm, in ZMA Por. 13446 it is 48–84–102 x 5–7.4–9 µm.

Distribution and ecology. Saudi Arabian Red Sea, Israelian Gulf of Aqaba, on reefs.

Remarks. The molecular sequence of the Jeddah specimen grouped with Voigt *et al.*'s *C. rowi* specimens (cf. Fig. 2A); no sequence for the Aqaba specimen was obtained. For that reason we present separate morphological data for the two available specimens. The shape of the cormus of the Jeddah specimen with the longer wider tubuli combined with a fine network of thinner tubuli is the same as in Voigt *et al.*'s type series. However, the shape (cylindroconical) and the size (up to 151 µm) of the triactines of the Jeddah specimen differ from the triactines of the type series, which has actines up to 103 µm long as described by Voigt *et al.* The Aqaba specimen has a comparable spicule size as the type series.

Sequence data for specimens assigned to *C. rowi* by Voigt *et al.* 2017 were not strongly separated from sequences we found in specimens which we assigned to *Clathrina luteoculcitella* Wörheide & Hooper, 1999 (cf. Fig. 2A). A larger clade with high bootstrap value unites our specimen and Voigt *et al.*'s (2017) specimens of *C. rowi*, with Indonesian and Australian specimens of *C. luteoculcitella* as well as with Rodrigues specimens assigned below to *C. luteoculcitella*. In a separate analysis, a trimmed alignment with length 395 sites of both species

comprising Australian (downloaded from the Sponge Barcode Project), Indonesian, Red Sea and Oman specimens of *C. luteoculcitella*, together 8 sequences, and 10 Red Sea sequences of *C. rowi* (most donated by Oliver Voigt, but including one of ours, RMNH 10002), showed nine non-conserved sites. Four of these sites showed a neat separation between *C. luteoculcitella* and *C. rowi*, the other 5 sites showed single specimen differences or a mixed set of differences.

***Clathrina luteoculcitella* Wörheide & Hooper, 1999**

Figures 18a–f, 19a–e, 20a–e

Clathrina luteoculcitella Wörheide & Hooper, 1999: 868, figs 5A–E

Clathrina aff. *luteoculcitella*; Van Soest & De Voogd 2015: 13, figs 6a–d.

Material examined. RMNH Por. 11623, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG024, 16 October 2016; RMNH Por. 11641, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG044, 17 October 2016; RMNH Por. 11659, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG063, 17 October 2016; RMNH Por. 11686, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG094, 18 October 2016; RMNH Por. 11687, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.7648°S 63.4626°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG101, 19 October 2016; RMNH Por. 11703, Mauritius, Rodrigues, Passe Saint François, 19.69893°S 63.5005°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. ROG117, 20 October 2016; ZMA Por. 17438, Oman, Muscat, Ras al Khayran, on rocks, 23.75°N 58.75°E, (depth not recorded, but shallow), scuba, coll. O. Eerland, field nr. 02/IO/DEC08/OE/006, 6 December 2002; ZMA Por. 10223b, Seychelles, Mahé, NE coast, Cap Maçons and Anse de Forbans, 4.7667°S 55.5167°E, depth 0–6 m, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 612, 12 December 1992.

Description. Cushion-shaped masses of tightly anastomosed tubuli (Figs 18a–e). Tubuli thin, 0.2–0.4 mm in diameter. Numerous prominent oscules much wider than individual tubuli are visible on the upper side on in situ images (e.g. Fig. 18a). Color beige or orange-brown in situ, dirty white or pale beige ‘on deck’, (Fig. 18f), pale beige in preserved condition. Consistency soft. Sizes up to 6 x 3 x 3 cm, individual tubuli 0.2–0.3 mm in diameter. The specimen from Oman had white live color, the Seychelles specimen was of unknown life color; both are pale beige (Fig. 20a) in preserved condition.

Aquiferous system. Asconoid.

Skeleton. (Figs 19a–b, 20b,d) Thin tubules with the walls single-spicule layered, not very dense. Spaces between the tubuli small, 0.1–0.5 µm.

Spicules. (Figs 19c–e, 20c,e) Triactines equiangular equiradiate, with small conical actines; some broken trichoxeas (Fig. 19d).

Measurements of the actines of the triactines in three of the specimens from Rodrigues show a very limited variation:

RMNH Por. 11641: 69–99 x 6.5–9.5 µm

RMNH Por. 11659: 72–94 x 6–9 µm

RMNH Por. 11687: 74–93 x 6–9.5 µm

Overall, sizes are 69–99 x 6–9.5 µm (n= 50).

Few broken trichoxeas are found in one of the specimens.

Triactines of the Oman specimen (Figs 20c) are slightly larger, 72–95.6–108 x 6.5–9.4–12 µm (n=25); those of the Seychelles specimen (Fig. 20e) are similar to the Rodrigues specimens: 71–84–96 x 7–8.6–9.5 µm (n= 25).

Distribution and ecology. Rodrigues, Oman, Australia, Indonesia, on reefs at 0–15 m depth.

Remarks. The identification of the Rodrigues specimens with *C. luteoculcitella* is based on morphological and molecular characters. The species is distinct by its cushion-shaped mass of tightly meshed tubuli in combination with prominent oscules and small conical-actined triactines. Partial 28S sequence data point towards close relationship with Indonesian specimen ZMA Por. 08657 assigned to *Clathrina luteoculcitella* (cf. Van Soest & De

Voogd 2015) and the Northeast Australian holotype of the species in the Sponge Barcode Project database. Together they form a sisterclade to a clade containing specimens of *C. rowi* (see Fig. 2A). *Clathrina rowi* is morphologically distinct from *C. luteoculcitella* as the cormus is more loosely organized and has different color. As reported above, the two show small but consistent molecular differences.

Likely members of *C. luteoculcitella* from Oman and the Seychelles have also a tightly meshed cormus and small spicules. The sequence of the Oman specimen matches closely with those of Rodrigues and Indonesian specimens of that species. However, the in situ color was noted as white, so some doubt is in order. The Seychelles specimen was very small and no sequence could be obtained, but what information we obtained makes membership of this species likely. We provide separate illustrations of the various specimens to support our conclusion that all are assumed to be conspecific.

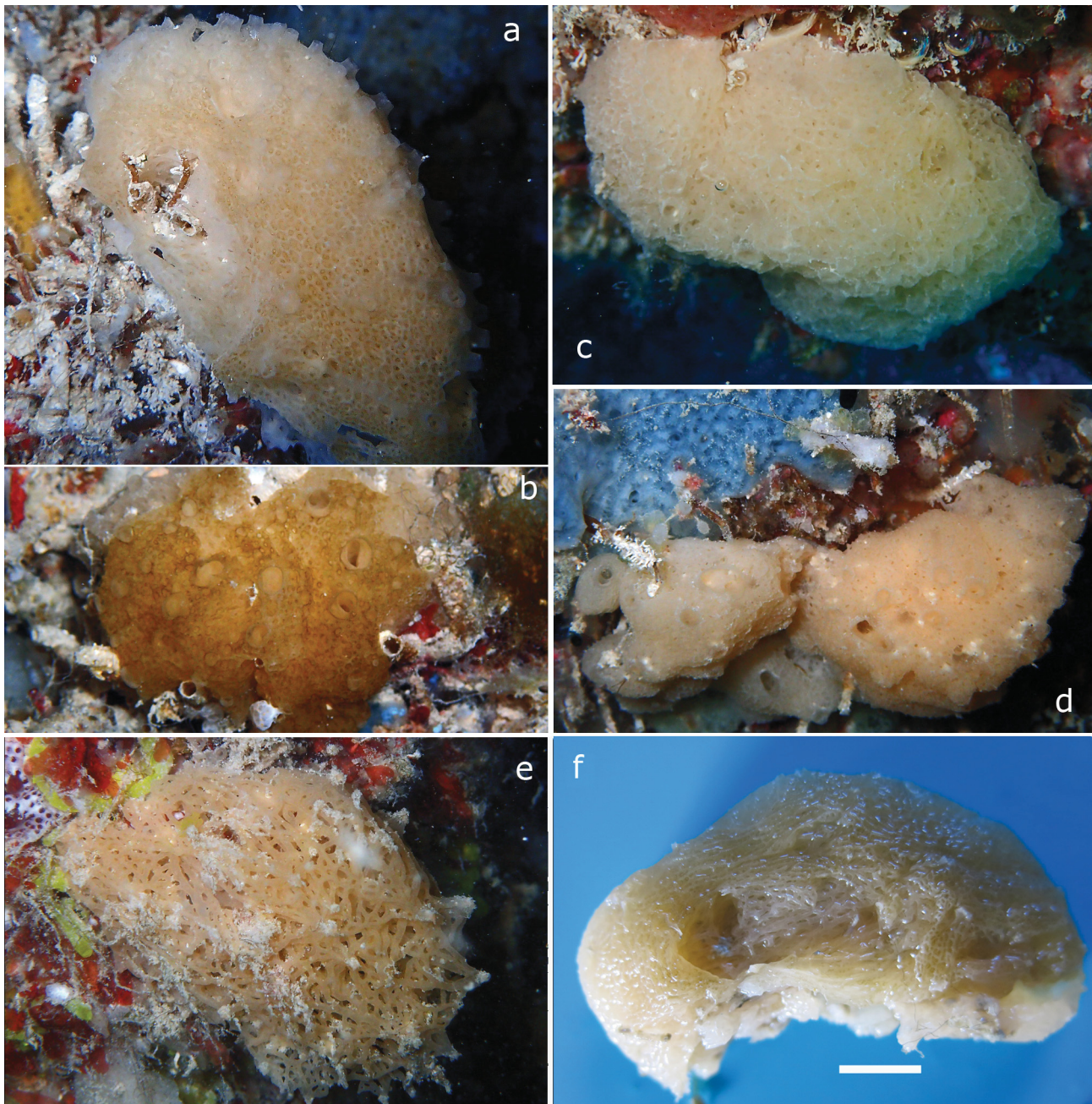


FIGURE 18. *Clathrina luteoculcitella* Wörheide & Hooper, 1999, habitus of various specimens from Rodrigues (all photos N.J. de Voogd), a, RMNH Por. 11641 (ROG044) specimen in situ, b, second specimen in situ of the same sample, c, RMNH Por. 11687 (ROG101) in situ, d, RMNH Por. 11703 (ROG117) in situ, e, RMNH Por. 11623 (ROG024), f, RMNH Por. 11641 specimen a on deck (scale bar = 1 cm).

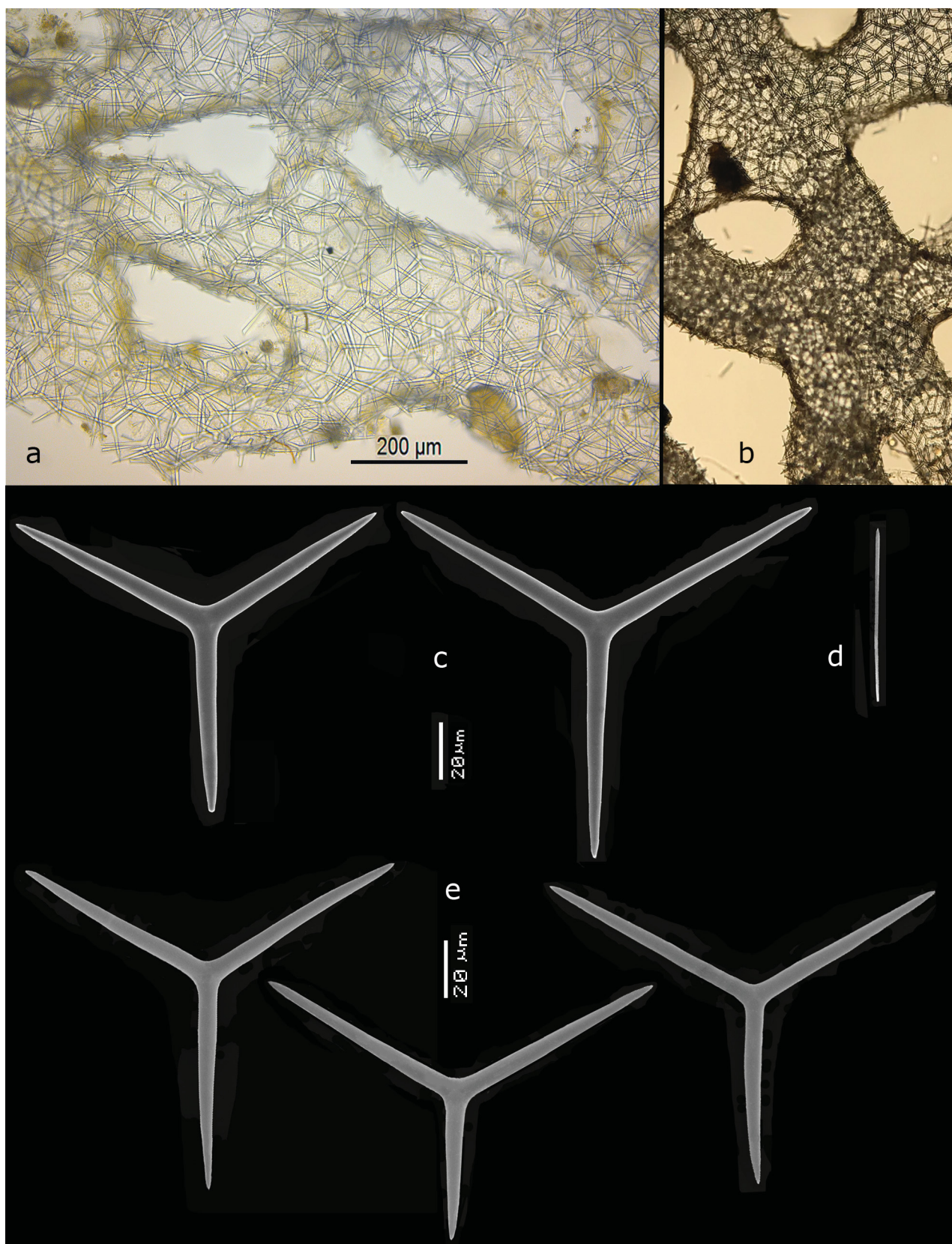


FIGURE 19. *Clathrina luteoculcitella* Wörheide & Hooper, 1999, from Rodrigues, skeleton and spicules, a–b, light microscopic images of the tubuli network, a, RMNH Por. 11687, b, RMNH Por. 11641, c–e, SEM images of spicules, c, triactines of RMNH Por. 11687, d, fragment of rare trichoxea of RMNH Por. 11687, e, triactines of RMNH Por. 11641.

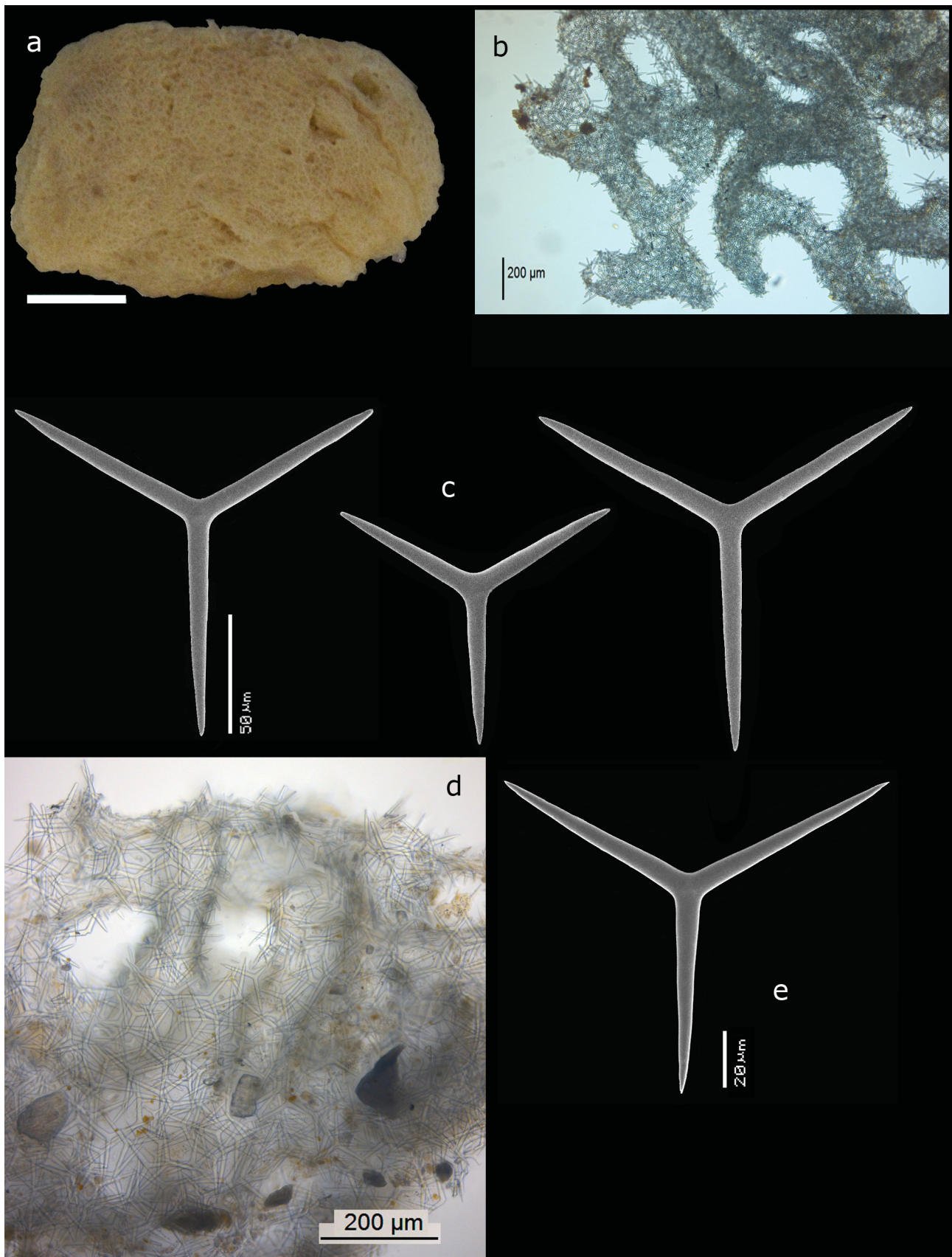


FIGURE 20. *Clathrina luteoculcitella* Wörheide & Hooper, 1999, a–c, ZMA Por. 17438, from Oman, a, preserved habitus (scale bar = 1 cm), b, light microscopical image of the tubuli reticulation, c, SEM images of the spicules, d–e, ZMA Por. 10223b, from the Seychelles, d, light microscopical image of the cornus, e, SEM image of triactine.

***Clathrina rodriguesensis* sp.nov.**

Figures 24a–e, 25a–g, 26a–d, 27a–d

Material examined. Holotype, RMNH Por. 11694, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.7648°S 63.4626°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG108, 19 October 2016.

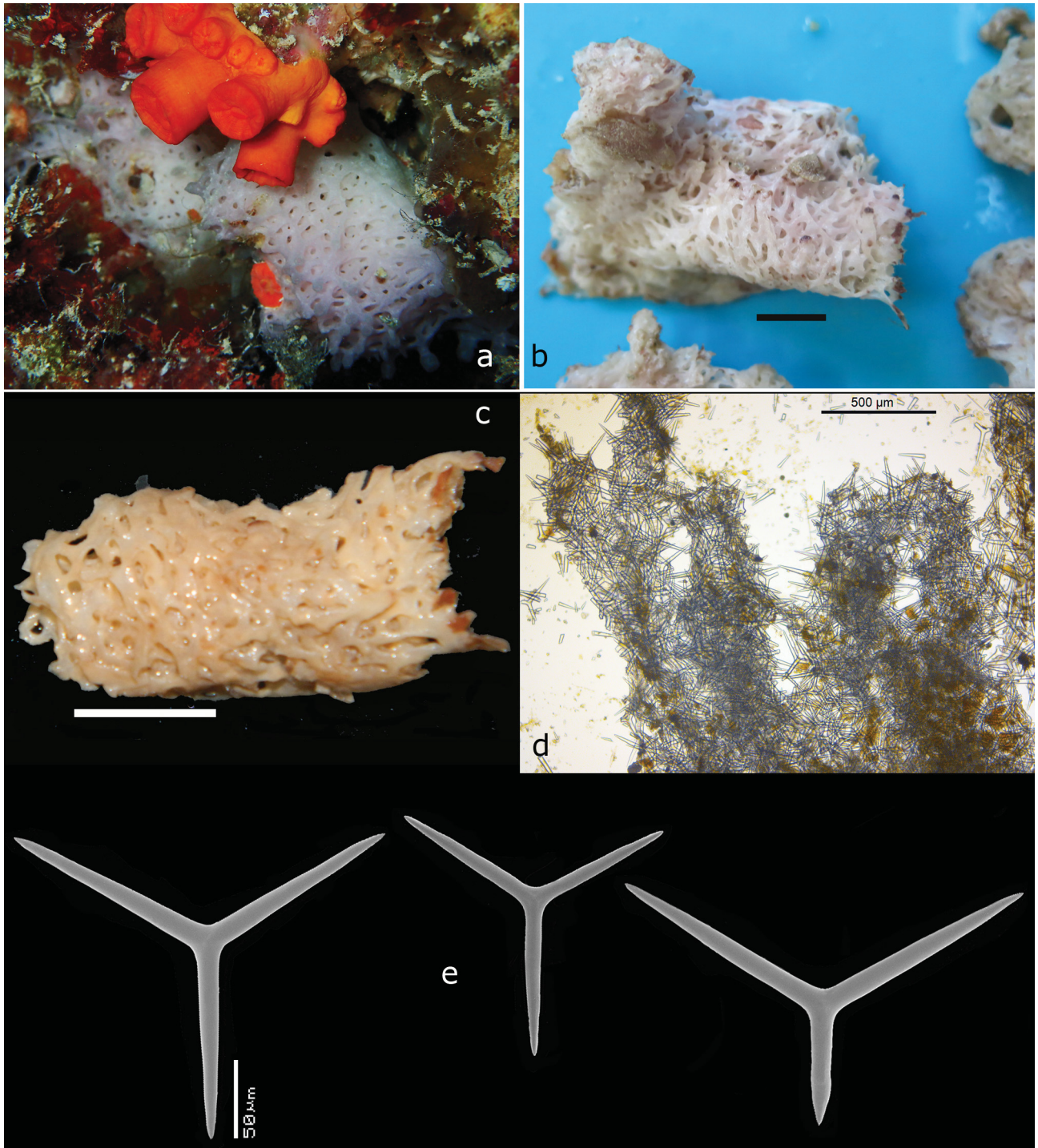


FIGURE 21. *Clathrina rodriguesensis* sp.nov., holotype RMNH Por. 11694, from Rodrigues, a, in situ (photo N.J. de Voogd), b, on deck (scale bar = 1 cm), c, preserved (scale bar = 1 cm), d, light microscopic image of the cormus, e, SEM images of the spicules.

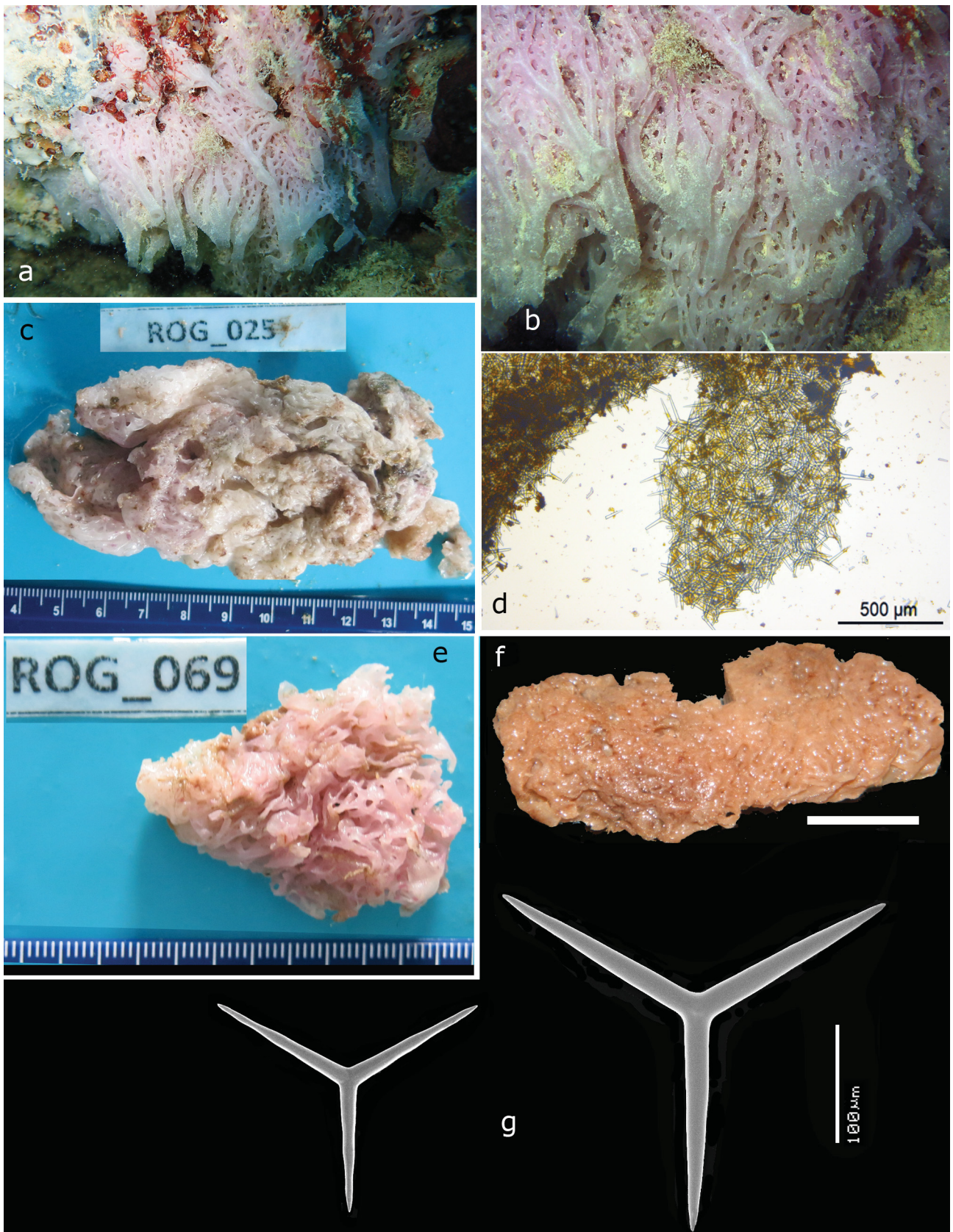


FIGURE 22. *Clathrina rodriguesensis* sp. nov., paratypes from Rodrigues, a–d, RMNH Por. 11662 (ROG025), a, in situ on the reefs (photo N.J. de Voogd), b, detail of a, c, on deck photo of the same, (photo N.J. de Voogd) d, light microscopic image of part of the cormus of the same, e–g, RMNH Por. 11662 (ROG069), e, on deck photo, f, preserved specimen of the same, g, SEM images of the spicules of the same.

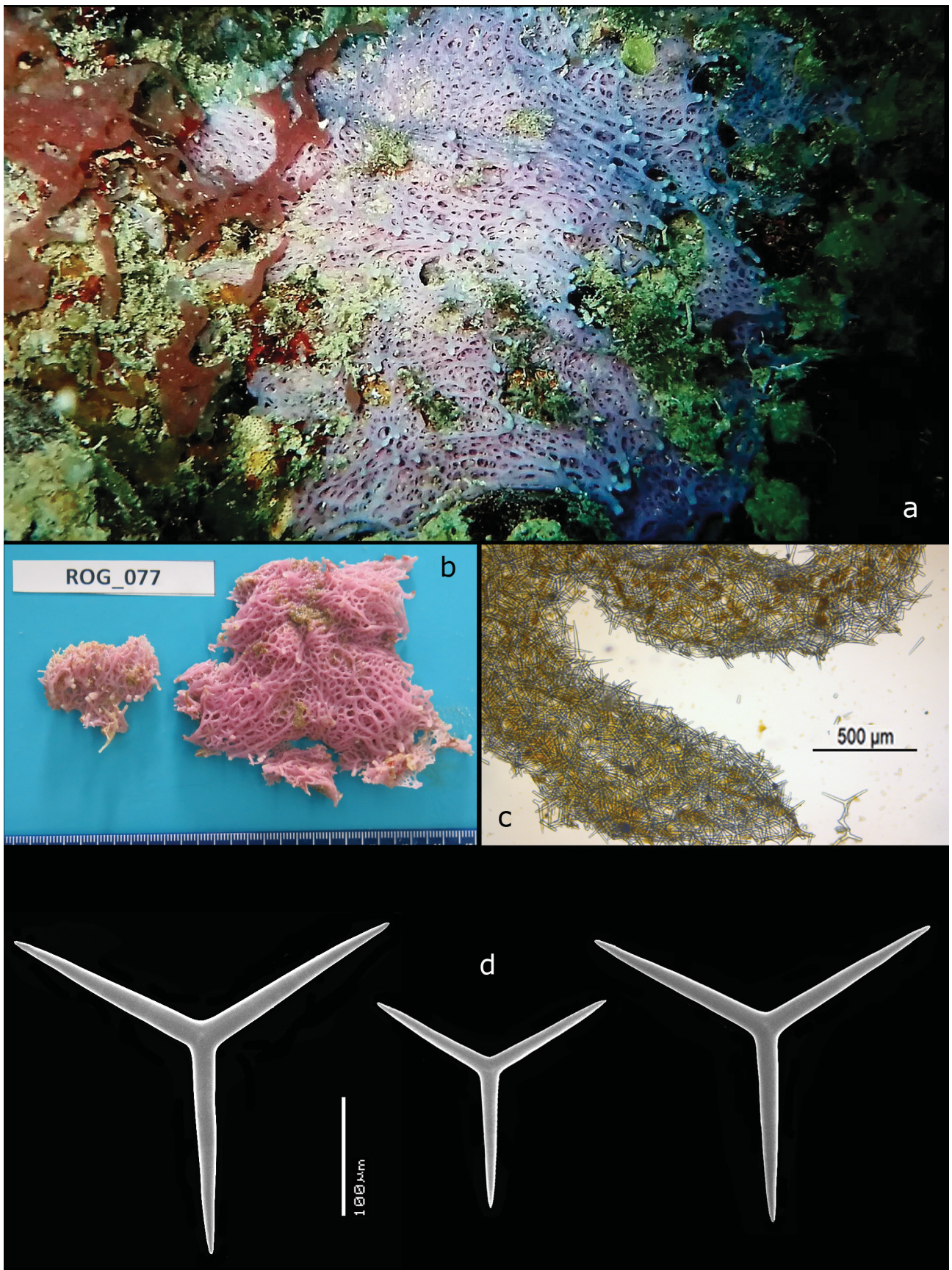


FIGURE 23. *Clathrina rodriguesensis* **sp. nov.**, paratype RMNH Por. 11670 from Rodrigues, a, habitus in situ (photo N.J. de Voogd), b, habitus on deck, c, light microscopic images of the tubuli network, d, SEM images of the spicules.

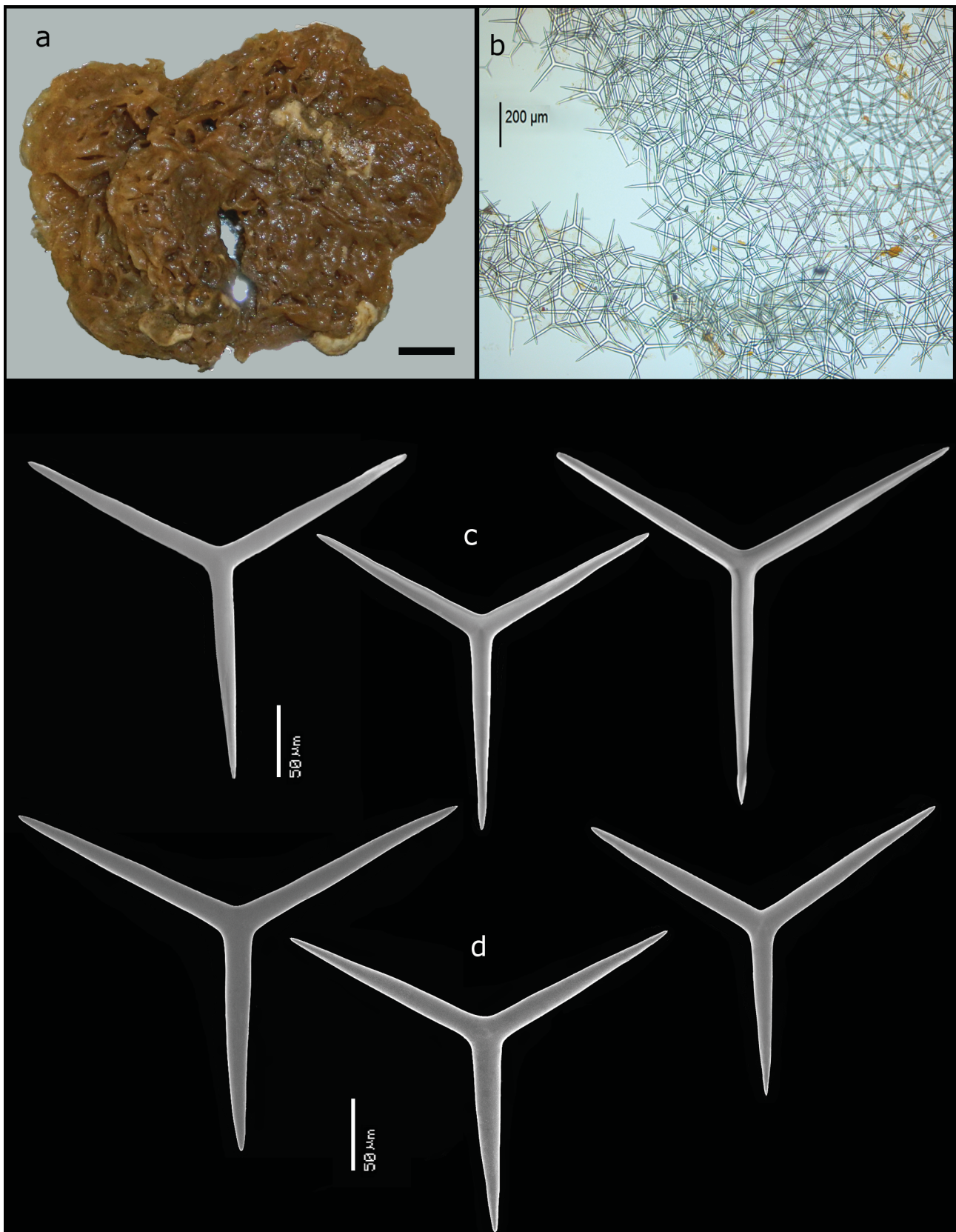


FIGURE 24. *Clathrina rodriguesensis* **sp.nov.**, specimens from the Seychelles, a, habitus of ZMA Por. 11282, preserved specimen (scale bar = 1 cm), b, light microscopic image of skeleton, c, SEM images of spicules, d, ditto of ZMA Por. 12096.

Paratypes, RMNH Por. 11624, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG025, 16 October 2016; RMNH Por. 11662, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG069, 18 October 2016; RMNH Por. 11670, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG077, 18 October 2016; RMNH Por. 11671, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG078, 18 October 2016; RMNH Por. 11705, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 8 m, scuba, coll. N.J. de Voogd, field nr. ROG119, 20 October 2016; RMNH Por. 11710, Mauritius, Rodrigues, Passe Saint François, 19.69893°S 63.5005°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. ROG124, 20 October 2016.

Additional specimens. ZMA Por. 11282, Seychelles, Amirantes, Desroches Atoll, SW rim, 5.7167°S 53.6167°E, depth 5–30 m, scuba, coll. M.J. de Kluijver, field nr. NIOP-E stat. 774/01, 30 December 1992; ZMA Por. 12096, Seychelles, Amirantes, St. François Atoll, Île Bijoutier, 7.0833°S 52.7333°E, reef, outer slope, depth 6–18 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 792/12, 5 January 1993.

Description. In situ, the species forms a massively encrusting cormus (Figs 21a–d, 22a–b) consisting of relatively wide tubuli (approximately up to 2–3 mm in diameter), which are nevertheless closely anastomosed, showing little differentiation in tubule-width. The cormus may be also flatly encrusting over a larger area (Fig. 23a) with loosely anastomosing tubuli showing a tendency to be arranged ladder-like, with longitudinal main tubuli and interconnecting secondary thinner tubuli. The main tubuli frequently end in an oscule, often slightly erected above the cormus (Figs 22a–b). Lateral size considerable, 20 x 15 cm or more, thickness 1–4 cm. Color white with blueish or greyish tinges in situ, white or pink ‘on deck’ (Figs 21b, 22c,e, 23b), in preservation they become pale beige (Figs 21c, 22f: Rodrigues specimens) or brown (Fig. 24a: Seychelles specimens). The latter have possibly become brown by exposure to algae or other sponges, as their in situ color was noted as blueish white. Size of preserved fragments up to 10 x 5 x 4 cm. Consistency firm.

Aquiferous system. Asconoid.

Skeleton. Tubule walls multi-layered, densely crowded in most specimens (Figs 21d, 22d, 23c), but less dense in one of the Seychelles specimens (Fig. 24b).

Spicules. (Figs 21e, 22g, 23d, 24c–d). Triactines only, but occasional fragments of trichoxea-like spicules were observed (not shown).

Triactines, robust, with conical actines, measuring 97–169–225 x 11–18.2–22 µm in the Rodrigues specimens. The two Seychelles specimens which we believe to belong to this species have actines respectively 93–159–198 x 11–17.4–21 µm (ZMA Por. 11282) and 111–164–204 x 13–17.8–21 µm (ZMA Por. 12096) (Figs 24c–d). The actines in all these specimens are conical

Distribution and ecology. Rodrigues, Seychelles, on reefs, 5–30 m depth.

Etymology. The name refers to the type locality, the island of Rodrigues, east of Mauritius.

Remarks. We provide ample illustrations of this new species to demonstrate the habitus variability. Spicules are closely similar in all above-mentioned specimens.

Partial 28S sequences of seven specimens collected at Rodrigues and two Seychelles specimens grouped in a separate clade (cf. Fig. 2A) at high bootstrap value, apparently not closely related to the other Western Indian Ocean *Clathrina*.

Australian and Indonesian *Clathrina heronensis* Wörheide & Hooper, 1999 is close in color and spicule size and shape, but its habitus is flatly encrusting and it has thinner tubuli (1 mm) than the present material. An Indonesian specimen identified as *C. heronensis* was sequenced and found to share a clade with lower bootstrap value with the present material in the molecular tree of Fig. 2A. A separate analysis of the sequences of both species in a trimmed alignment with length of 395 sites showed a difference of eight sites between *C. heronensis* and *C. rodriguesensis* **sp.nov.**

***Clathrina maremeccae* sp.nov.**

Figures 25a–c

Material examined. Holotype, RMNH Por. 9662, Saudi Arabia, Jeddah, near Thuwal, Um Albalam, 22.193556°N 38.9475°E, scuba, coll. N.J. de Voogd, field nr. THU10/JED166, 12 November 2014.

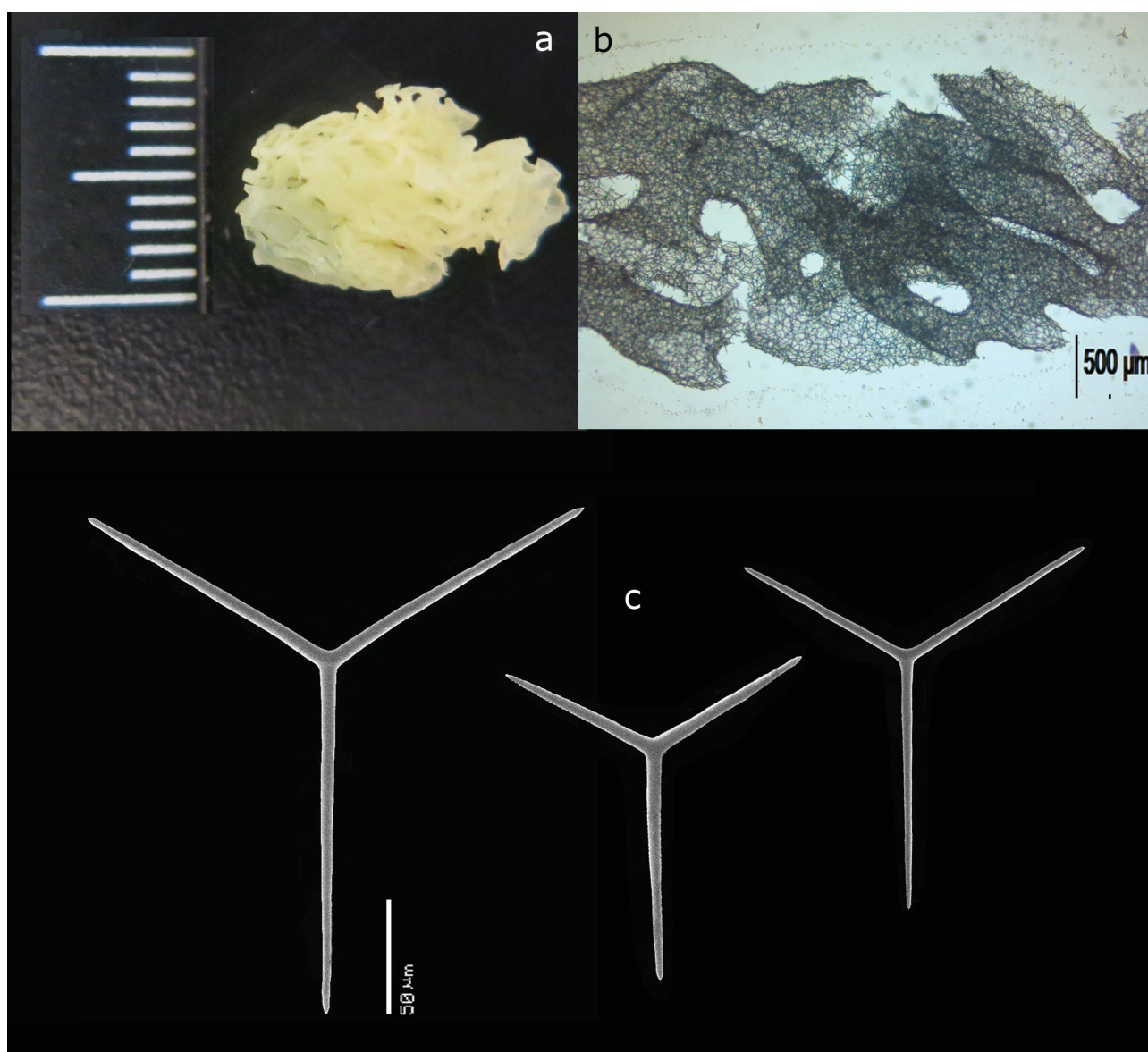


FIGURE 25. *Clathrina maremeccae* sp.nov., holotype RMNH 9662 from Saudi Arabia, Jeddah, a, habitus on deck (photo N.J. de Voogd), b, light microscopic image of the cormus, c, SEM images of triactines.

Description. Cormus clathroid (Fig. 25a), forming a loosely anastomosed small mass of tubuli 0.2–1 mm in diameter leading to a few wider oscules. The single specimen is 15 x 8 x 4 mm in size. No evident water-collecting tubes. Color pale yellow, based on an on deck photo as there is no in situ photo.

Skeleton. (Fig. 25b) The tubule walls have a single layer of overlapping triactines.

Spicules. (Figs 25c) Equiradiate and sagittal triactines, with cylindrical actines, ending in often slightly swollen, blunt endings. Actines 67–127.8–165 x 5–6.4–7.5 µm. A few broken trichoxeas are considered foreign.

Distribution and ecology. Saudian part of the Red Sea, on reefs.

Etymology. The name refers to the type locality, the Red Sea, which was named Mare Mecca by historical geographers (Wikipedia.org).

Remarks. The new species resembles Red Sea *Clathrina rotundata* Voigt *et al.*, 2017 both in morphological aspects (loosely clathroid and with cylindrical actines of the triactines), and in a molecular sense as this species, based on partial 28SrRNA, also falls outside the larger clades of *Clathrina* species in our phylogenetic tree of Western Indian Ocean *Clathrina* species (Fig. 2A). However, there are also compelling reasons not to assign the present specimen to *C. rotundata*. Morphologically, the on deck photo shows a pale yellow color, whereas *C. rotundata* is white, and the upper actine length of the triactines is considerably higher than that of *C. rotundata*.

(165 vs. 123 μm). Molecularly, according to our phylogenetic analysis, the two species are not closely related. In a separate trimmed alignment of the two species of 382 sites length, *C. maremeccae* **sp.nov.** and *C. rotundata* differed in 49 sites.

There is considerable morphological similarity with Indonesian *Clathrina beckingae* Van Soest & De Voogd, 2015, which has the same shape and tube diameter, colors also white and cream in various specimens, and equiradiate triactines with cylindrical actines. Differences are the presence of distinct water-collecting tubes and the absence of sagittal spicules in *C. beckingae*. Actine sizes of the triactines are also considerably smaller than those in *C. maremeccae* **sp.nov.** (up to 103 μm in *C. beckingae*). We obtained partial 28S rRNA sequences for this Indonesian material, and found that it differed in a separate trimmed 28S rRNA alignment of 382 sites length in 26 different sites.

No closely related species were identified in our partial 28S rRNA tree (Fig. 2A).

At the suggestion of one of the reviewers, we obtained an ITS sequence (not submitted to GenBank) for this species and in an analysis (not shown here) of ITS sequences of *Clathrina* species that appeared highly similar in a BLAST attempt, downloaded from GenBank, we noted that the new species ended up in a highly supported clade with *Clathrina* sp. 4 and sp. 5 sensu Klautau *et al.* 2013, respectively a species from the Caribbean and from French Polynesia. A trimmed alignment of 556 sites of the three species showed 35 site differences between *C. maremeccae* **sp.nov.** and *C. sp. 4*, and 21 site differences with *C. sp. 5*.

***Clathrina repens* sp.nov.**

Figures 26a–d

Material examined. Holotype, RMNH Por. 10161a, Maldives, Faafu Atoll, Wallstreet, 3.119°N 72.979556°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. MAD10/MAS122, 20 February 2015.

Description. Open network of creeping and upright tubuli, covering the surface of a keratose sponge (*Hyrtios* sp.) (Fig. 26a), size several cm^2 . A second specimen (Fig. 26a1, not collected) encrusted an ascidian. Individual tubuli approximately 2 mm high and 1 mm diameter. Upright tubuli often open-ended, presumed to be oscules. Color shades of dull orange, pink-orange and beige; pale beige in preservation (Fig. 26b).

Aquiferous system. Asconoid.

Skeleton. (Fig. 26c) Walls of tubuli with a single layer of spicules.

Spicules. (Fig. 26d) Triactines with conical actines, variable in length, 66–97–129 x 6–7.4–9 μm .

Distribution and ecology. Maldives, coral reef, 10 m.

Etymology. *Repens* (L.) means creeping, referring to the reticulation of small tubuli closely adhering to the substratum.

Remarks. Morphologically, this appears a unique species. Its habitus and spicule sizes show similarity to Indonesian *Arturia tubuloreticulata* Van Soest & De Voogd, 2015, but this has a minority of tetractines. We examined the present specimen exhaustively, but could find no tetractines.

Unfortunately, no sequences were obtained from it.

***Clathrina* aff. *pulcherrima* (Dendy, 1891)**

Figures 27a–e

? *Leucosolenia pulcherrima* Dendy, 1891: 52, pl. I fig. 7, pl. IV fig. 3, pl. X fig. 3.

? *Clathrina blanca*; Jenkin 1908: 438, figs 85–87 (not: Miklucho-Maclay 1868)

? *Clathrina blanca* f. *pulcherrima*; Borojević 1967: 191 (? not: Dendy 1891)

Material examined. ZMA Por. 22408c, Mozambique Channel, between Mozambique and Madagascar, E of Juan de Nova Island, 17.2817°S 43.1567°E, depth 60 m, trawl, coll. RV 'Pelagia' Around Africa II expedition, field nr. 20-ASC10, 1 April 2001.

Description. Stalked *Guancha*-like sponge with flattened cormus (Fig. 27a) consisting of a tightly anastomosed mass of thin tubuli. The upper rim of the cormus has a row of tiny oscules (Fig. 27a1). Size entire specimen 3.3 cm high, stalk 1.8 cm long and 0.17 cm thick, cormus 1.3 cm wide, 0.4 cm thick. Tubuli about

0.05–0.1 mm in thickness, with thicker tubuli running the entire length of the cormus. Color in alcohol dirty white to light beige.

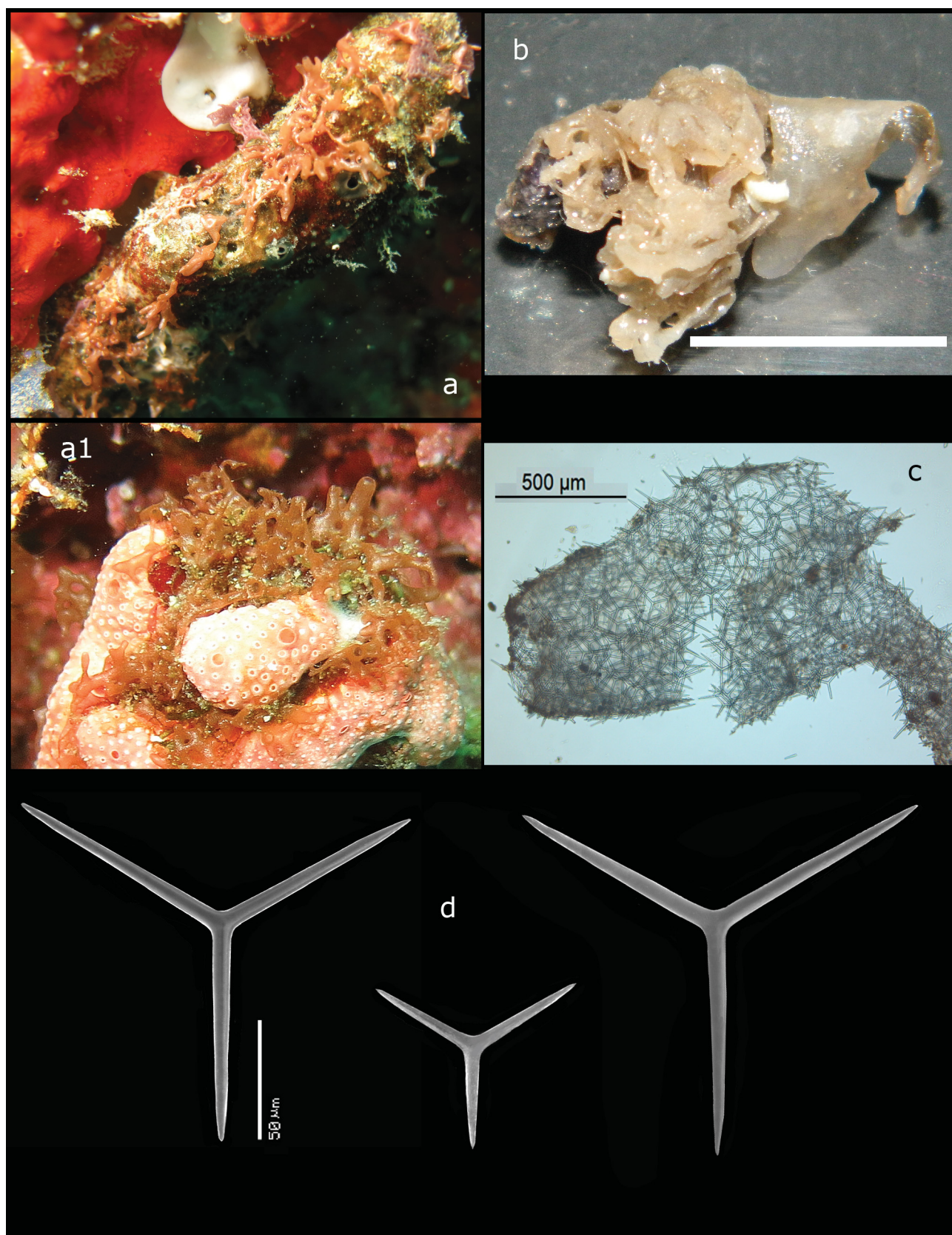


FIGURE 26. *Clathrina repens* sp.nov., a, in situ habitus of holotype RMNH Por. 10161 from the Maldives, a1, in situ habitus of a second specimen (not collected) (photos N.J. de Voogd), b, preserved holotype (scale bar = 1 cm), c, light microscopic image of one of the tubuli, d, SEM images of the spicules.

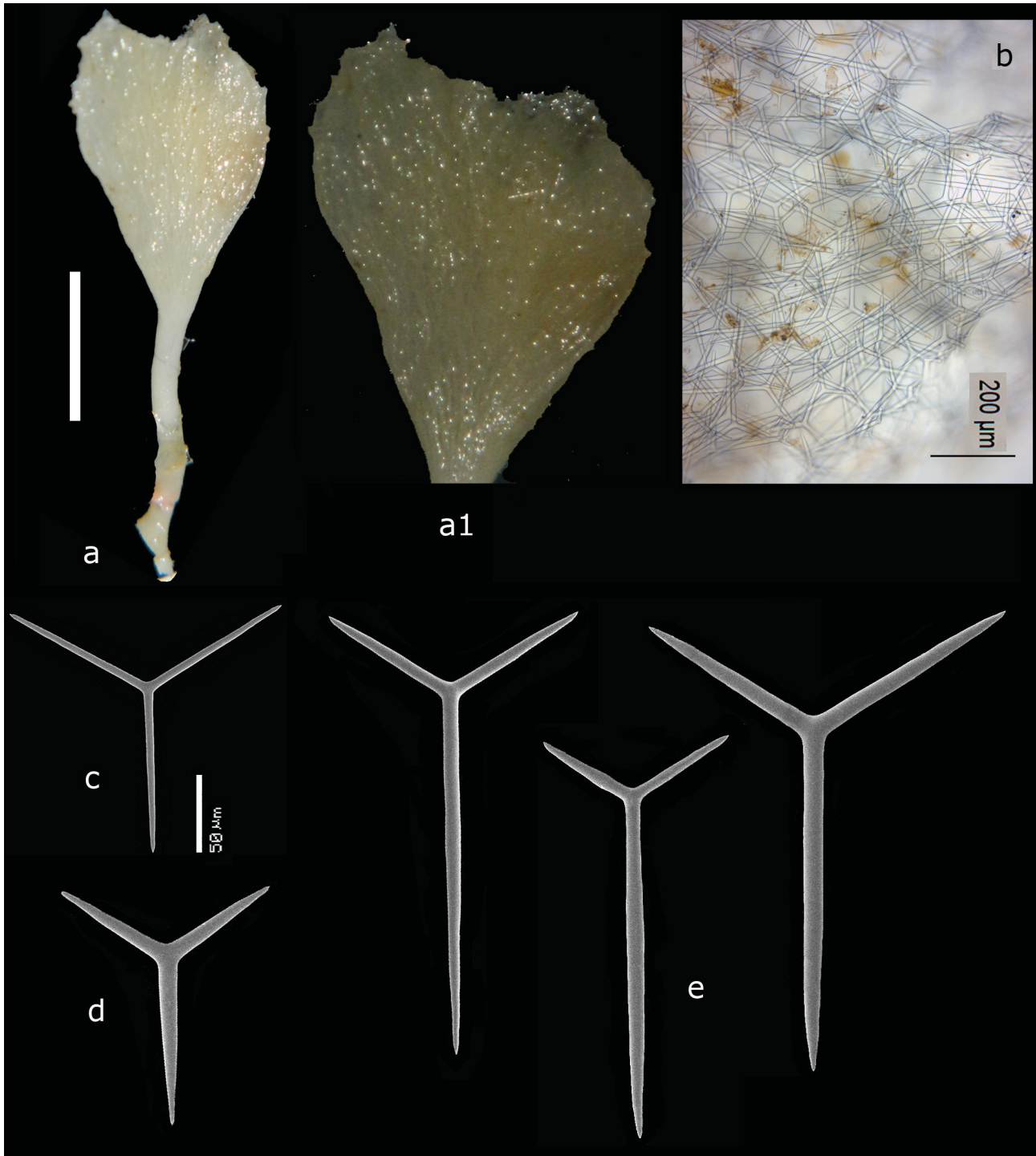


FIGURE 27. *Clathrina* aff. *pulcherrima* (Dendy, 1891), a, habitus of preserved specimen from Mozambique Channel W of Madagascar (scale bar = 1 cm), a1, detail of head with row of oscules on the rim, b, light microscopic image of skeleton of the basal part of the head, showing aligned parasagittal spicules, c–e, SEM images of the spicules, c, equiradiate triactine with thin actine, d, ditto with thick conical actines, e, various shaped parasagittal triactines.

Aquiferous system. Asconoid.

Skeleton. (Fig. 27b) Stalk and outer tubule walls consist of strongly sagittal triactines and to a lesser extent regular triactines; inner tubuli predominantly have regular triactines in their walls.

Spicules. (Figs 27c–e) Triactines only.

Triactines, in two distinct types, (1) equiradiate equiactinal triactines (Fig. 27c) with thin cylindrical actines 59–101–126 × 5–6.3–8 µm, occasionally slightly sagittal with thicker conical actines (Fig. 27d), and (2) strongly

sagittal (parasagittal) triactines (Figs 27e), with conical actines, with unpaired actines usually thicker halfway, paired actines usually tapering gradually, but occasionally also thicker halfway, unpaired actines strongly variable in length, 151–226–267 x 7.5–11.5–13 µm, paired actines 61–114–140 x 7–10.1–12 µm.

Distribution and ecology. Mozambique Channel, possibly SE coast of South Africa, possibly Southeast Australia, shallow water to 60 m depth.

Remarks. The shape of this specimen closely resembles the description and drawing of the Southeast Australian species *Clathrina pulcherrima* Dendy, 1891 (see Dendy, 1891, p. 52, pl. I fig. 7, as *Leucosolenia*). This is likewise a stalked sponge with upper body of laterally compressed oval shape, with the upper rim provided with a row of oscules. The spicules are also divisible in regular equiradiate and equiangular triactines and parasagittal triactines. However, there is a significant difference in the lengths of the actines: the equiradiate actines measure 84 x 4.2 µm, the parasagittal unpaired actines are 100 x 8 µm long and the paired actines are 56 x 8 µm. Although Dendy did not give ranges of the actines, it is clear from these data that the spicules are distinctly shorter and thinner than the present ones. It is currently judged to be uncertain whether this difference merits specific distinction.

Jenkin (1908) reported a flattened specimen of *Clathrina blanca* (Miklucho-Maclay, 1868) from Zanzibar, which reminds of our specimen, but is more irregular and the stalk is not a separately developed structure. It likewise has two types of triactines, regular triactines with actines of 60–100 x 4–9 µm and sagittal triactines with long unpaired actines of 100–160 x 7–11 µm. These measurements are somewhat inbetween those of Dendy and ours. *Clathrina blanca* is not flattened and is confined to the North Atlantic.

Borojević (1967) described specimens from South Africa (East London and Durban) as *Clathrina blanca* forma *pulcherrima*, but since he did not give spicule measurements, nor illustrations, it is not certain his specimens belonged to the same species as the present. He also signaled the presence of tripods, shaped similar to the regular triactines but with raised centre, which were not clearly present in the above-described specimen.

Haeckel (1872) reported (p. 16) and illustrated (his pl. 2 figs 5 and 6) stalked *Clathrina primordialis* specimens from the Red Sea, which he obtained from Miklucho-Maclay with the manuscript name '*Nardoa arabica*'. The specimens had only a single oscule and the spicules were all regular triactines. Row (1909) also reported *C. primordialis* but gave no description or illustration. Recently, Klautau *et al.* 2016 redescribed *C. primordialis* from the Adriatic and restricted that species to the Mediterranean. The identity of the Red Sea population referred to by Haeckel and Row remains uncertain. Voigt *et al.* 2017 stated that it possibly was conspecific with their *Clathrina rowi*.

Although there is no morphological similarity, molecular sequence analysis of partial 28SrRNA put this species closest to *Clathrina rotundata* Voigt *et al.*, 2017. Still, a trimmed alignment with length of 395 sites showed 45 site differences between the present species and *C. rotundata*. This result merely expresses the isolated positions of these two species.

Guancha Miklucho-Maclay, 1868, for a long time used for stalked *Clathrina*-type sponges, has been synonymized with *Clathrina* s.s. because its type species *C. blanca* conforms to the new definition of *Clathrina*. However, it is quite possible that a species group of that genus with the combination of stalked habitus and differentiated regular and long-unpaired actine sagittal triactines deserves to be recognized at the genus level. This is not further elaborated here.

Genus *Ernstia* Klautau *et al.*, 2013

Ernstia arabica Voigt *et al.*, 2017

Figures 28a–c, 29a–c, 30a–e

Ernstia arabica Voigt *et al.*, 2017: 9, figs 5a–e.

Material examined. ZMA Por. 13640, Israel, Coral Garden, Gulf of Aqaba, depth 1.5 m, scuba, coll. M. Wunsch, field nr. AQ140, 15 July 1998; ZMA Por. 13642, Egypt, Ras Mohammed, Shark Observatory, depth 15 m, scuba, coll. M. Wunsch, field nr. RM222, 23 July 1998.

Description. There are two, rather different specimens from the Gulf of Aqaba, which are assumed to be

members of this species. Because of the differences we describe them separately. Cormus of ZMA Por. 13640 (Fig. 28a) small yellow cushions connected by thinner stolon-like parts, structure compact made up of tightly anastomosed thin tubuli (Fig. 28b). Oscules centrally located on the cushions and slightly elevated. Lateral size of cormus up to 2.5 x 1 cm, thickness about 5–8 mm. ZMA Por. 13642 is a flatly encrusting cormus (Fig. 30a) consisting of tightly anastomosed thin tubuli. Pale yellow in life, dirty white in alcohol. Several broader tubuli lead to a few wide oscules slightly raised above the cormus. Lateral size 5 x 4 cm. Consistency soft.

Aquiferous system. Asconoid.

Skeleton. (Figs 28b–e) Walls of tubuli in both specimens are thin (Fig. 28c), consisting of one–two spicule layers (Figs 28d, 30b) with a mixture of tri- and tetractines; the apical actines of the latter are protruding into the tubule lumina (Fig. 28c) forming a dense palisade (Fig. 28e). Consistency firm.

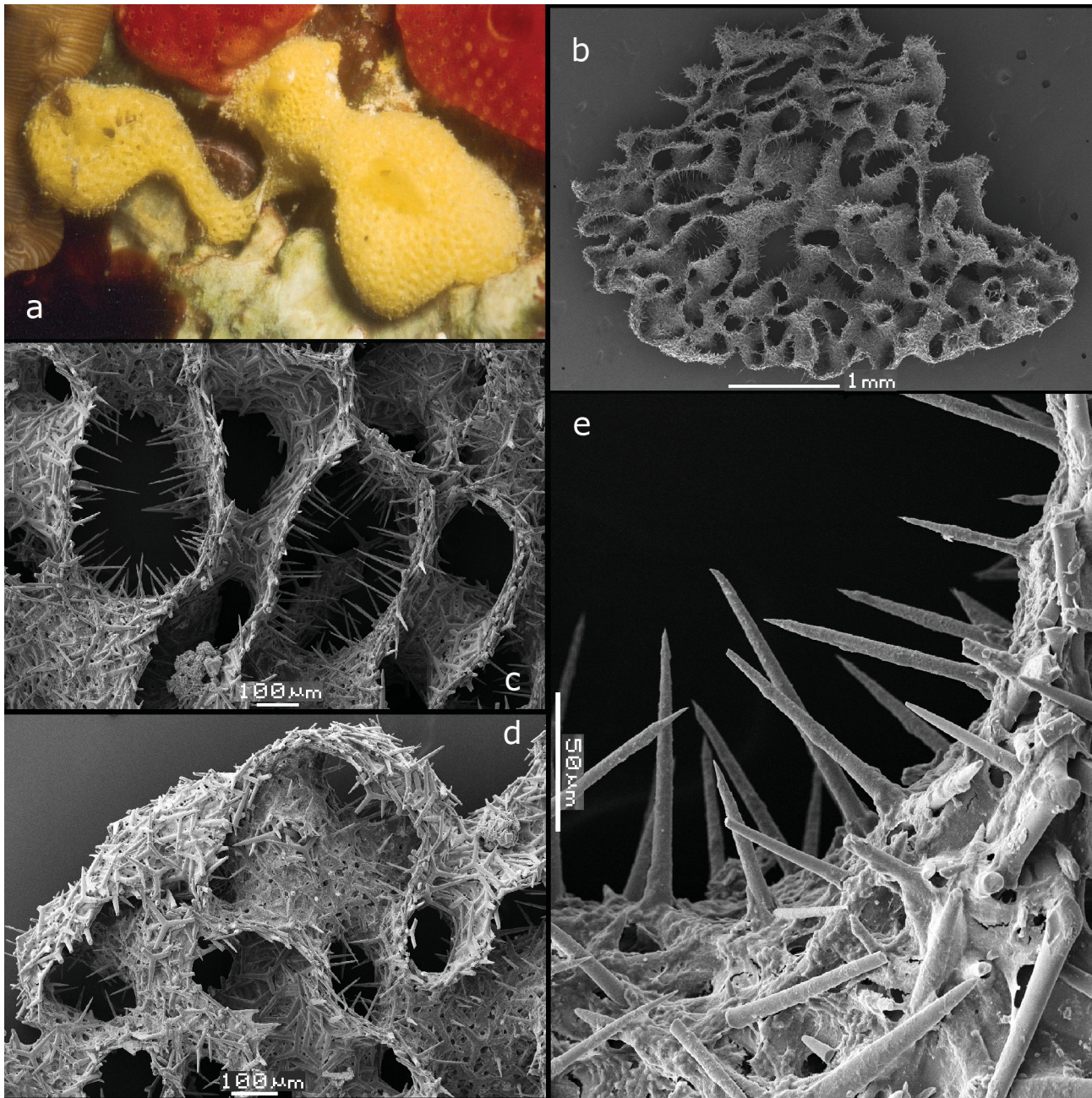


FIGURE 28. *Ernstia arabica* Voigt *et al.* 2017, ZMA Por. 13640, from the Gulf of Aqaba, a, habitus in situ (photo M. Wunsch), b–e, SEM images of sections of the cormus, b, overall section showing tightly anastomosed tubuli, c, cross section of tubuli showing apical actines of tetractines protruding in the tubar lumen, d, cross section of the surface region, e, detail of tubar lumen and protruding apical actines.

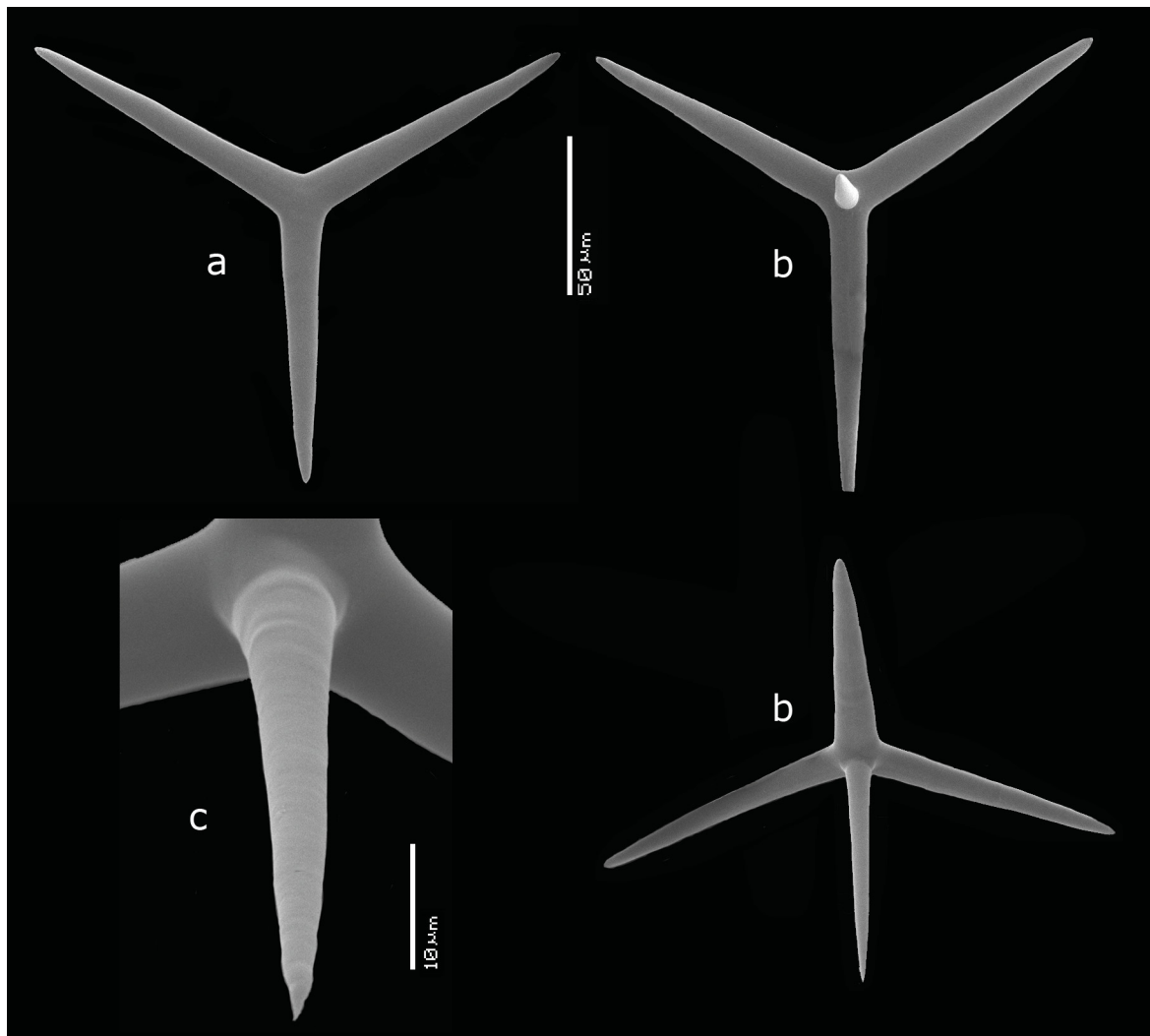


FIGURE 29. *Ernstia arabica* Voigt *et al.* 2017, ZMA Por. 13640, from the Gulf of Aqaba, SEM images of the spicules, a, triactine, b, tetractines, c, detail of apical actine of tetractine.

Spicules. (Figs 29a–c, 30c–e) Triactines and tetractines, the latter present in clearly larger numbers. No distinct trichoxeas were found.

Triactines equiradiate and equiangular, with conical actines, some verging toward tripod-shape.

Actine sizes of ZMA Por. 13640 (Fig. 29a) measure 89–98–105 x 9–11.2–13 µm.

Actine sizes of ZMA Por. 13642 (Figs 30c) measure 102–125–165 x 11–16.4–26 µm.

Tetractines of similar shape and size to the triactines, equiangular, with conical actines.

Actines of the basal triactate system in ZMA Por. 13640 (Figs 29b) measure 87–94–99 x 9–10.3–12 µm, apical actines (Fig. 30c) smooth, straight, 66–76–91 x 5–6.6–8 µm.

Actines of the basal triactate system in ZMA Por. 13642 measure (Figs 30d) 67–127–182 x 9–15.2–27 µm; apical actines (Fig. 30e) shorter, thinner and sharper, 23–38–59 x 3–5.7–11 µm.

Distribution and ecology. Israelian Red Sea, Saudi Arabian and Egyptian Red Sea (Voigt *et al.* 2017), down to 15 m.

Remarks. The present specimens closely resemble the type in most aspects, except for the absence of trichoxeas. These were also not consistently present in the type material (Voigt *et al.* 2017). A small further difference is the length of the apical actine of the tetractines, which has a greater range in the type material (up to 156 µm). The two present specimens differ subtly in the habitus and the smaller-thinner vs. the larger and more robust spicules. Voigt *et al.* (2017) described and measured the spicules of specimens from the Northern and Southern Red Sea and found triactines and tetractines having actine lengths between 38 and 116 µm, and apical actines between 56 and 156 µm, while our own specimens have these data respectively 67–182 µm and 23–91 µm.

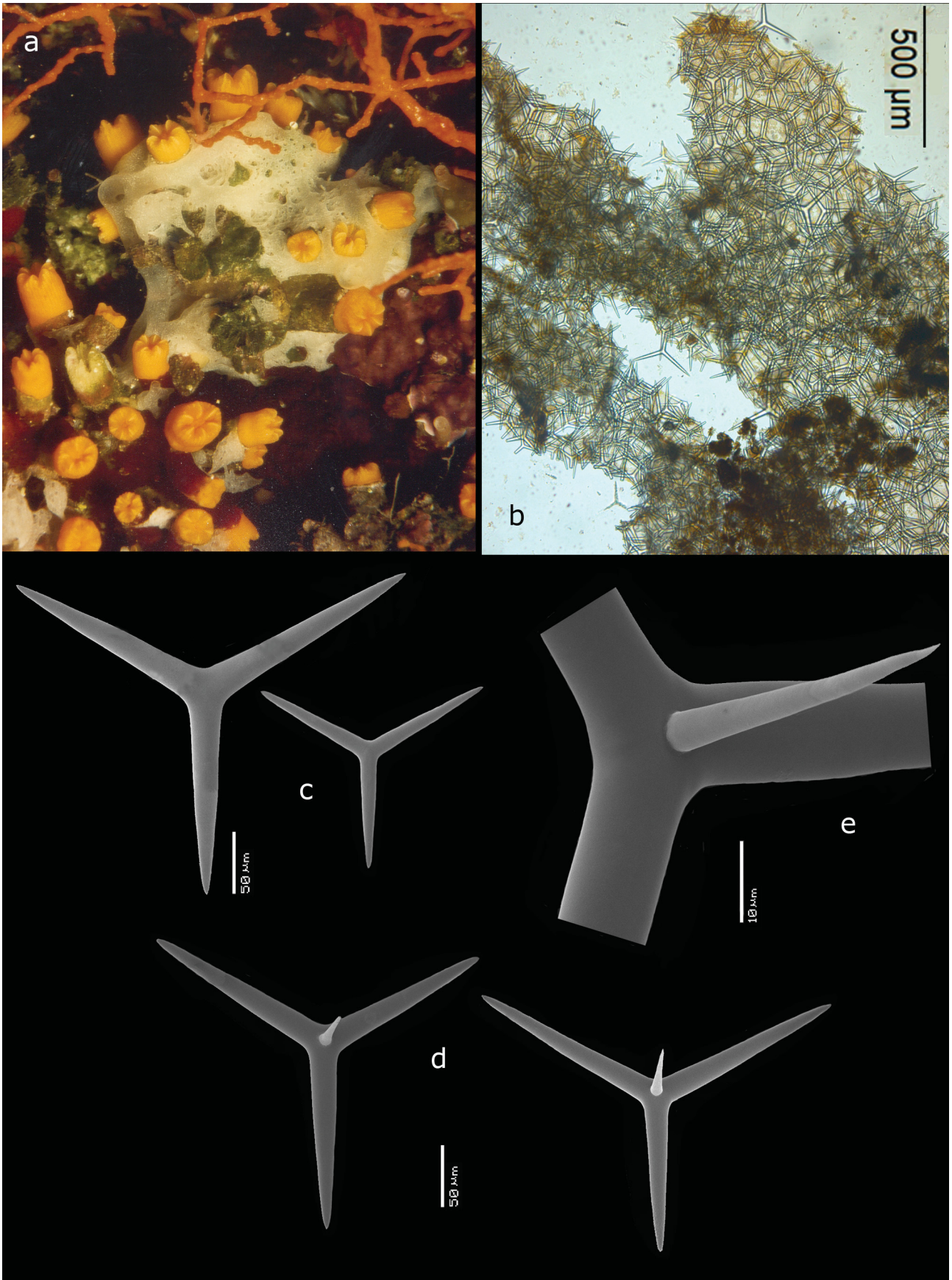


FIGURE 30. *Ernstia arabica* Voigt *et al.* 2017, ZMA Por. 13642, from Northern Red Sea, Egypt, Ras Mohammed, a, habitus in situ on the reef (photo M. Wunsch), b, light microscopic image of a detail of the cormus, c–e, SEM images of the spicules, c, triactines, d, tetractines, e, detail of apical actine of tetractine.

Unfortunately, we were unable to obtain partial 28S rRNA sequences for these specimens. Below we compare *E. arabica* with Western Indian Ocean specimens identified as the closely related *Ernstia naturalis* Van Soest & De Voogd, 2015.

***Ernstia naturalis* Van Soest & De Voogd, 2015**

Figures 31a–f, 32a–g, 33a–d, 34a–c

Ernstia naturalis Van Soest & De Voogd, 2015: 28, figs 20–21.

Material examined. RMNH Por. 11612, Mauritius, Rodrigues, Passe Grenade, 19.67503°S 63.48422°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG013, 16 October 2016; RMNH Por. 11614, Mauritius, Rodrigues, Passe Grenade, 19.67503°S 63.48422°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG015, 16 October 2016; RMNH Por. 11629, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG030, 16 October 2016; RMNH Por. 11633, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG034, 16 October 2016; RMNH Por. 11660, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG066, 18 October 2016; RMNH Por. 11667, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. ROG074, 18 October 2016; RMNH Por. 11702, Mauritius, Rodrigues, Passe Saint François, 19.69893°S 63.5005°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. ROG116, 20 October 2016; RMNH Por. 11719, Mauritius, Rodrigues, Passe Baladirou, 19.6683°S 63.46307°E, depth 8 m, scuba, coll. N.J. de Voogd, field nr. ROG133, 20 October 2016; RMNH Por. 8444, France, Mayotte, Baie de Bouenie (île), 12.9183°S 45.1384°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. MAY13-144, 9 May 2013.

Description. We describe and illustrate the Rodrigues specimens separate from a single large specimen collected at Mayotte, because there is a slight discrepancy in shape, spicules and sequences (cf. below). The Rodrigues specimens (Figs 31a–d) have a thickly encrusting cormus, adhering to vertical rock walls and hanging down from cave ceilings. The cormus consists of loosely anastomosed relatively coarse tubuli of bright or dull yellow color. Size of entire cormus measured on deck (Fig. 31e) is up to 7 x 5 x 3 cm. Tubuli up to 6 mm in diameter. Distinct watercollecting tubes are slightly wider than the anastomosing tubuli. In preserved condition pale beige (Fig. 31f), and usually considerably shrunken. Consistency soft.

The habitus of the Mayotte specimen (Fig. 33a) is a lobate, laterally compressed, anastomosed mass of moderately wide tubules of pale yellow color. Distinct water collecting tubes lead to wide oscules at the crown of each lobe. Preserved specimen (Fig. 33b) a thickly compressed mass 3 x 2 x 2 cm, color brownish. Individual tubules 0.2–1 mm diameter (preserved condition, distinctly wider in situ).

Aquiferous system. Asconoid.

Skeleton. Tubule wall of Rodrigues specimens (Figs 32a–d) densely spiculated. The Mayotte specimen is similar (Figs 33c–d). Open spaces between the anastomosed tubules 0.2–1 mm in size, tubule walls 20–50 µm in thickness, several spicule layers thick.

Spicules. (Figs 32c–g, 34a–c) Triactines and tetractines, (broken) trichoxeas are found in most specimens. Tetractines are the most common spicules.

Triactines (Rodrigues, Figs 32c,f; Mayotte, Figs 34a) equiradiate and equiangular, with conical actines.

Actine sizes in five Rodrigues specimens:

RMNH Por. 11612: 84–102–119 x 8.5–9.4–12 µm

RMNH Por. 11660: 78–101–120 x 7–9.6–11 µm

RMNH Por. 11667: 84–101–114 x 8–9.5–12 µm

RMNH Por. 11702: 82–102–114 x 7–8.9–11 µm

RMNH Por. 11719: 78–106–138 x 8–9.1–12 µm

In one Mayotte specimen, actines notably thicker than the Rodrigues specimen, occasionally with one of the actines shorter:

RMNH Por. 8444: 108–124–138 x 11.5–13.3–15 μm .
Combined size data: 78–138 x 7–15 μm

Tetractines (Rodrigues, Figs 32d,g; Mayotte, Figs 34b,d) with basal radiate system similar to the triactines, with apical actines straight, conical, usual thin, and occasionally longer than the basal actines.

Actines of the basal radiate system in five Rodrigues specimens:

RMNH Por. 11612: 72–104–118 x 7–9.3–11 μm
RMNH Por. 11660: 93–100–124 x 7–10.3–12 μm
RMNH Por. 11667: 83–99–120 x 7.5–9.5–11 μm
RMNH Por. 11702: 87–104–115 x 7.5–8.9–11 μm
RMNH Por. 11719: 79–108–123 x 8.5–9.6–11 μm

In one Mayotte specimen, actines notably thicker than the Rodrigues specimen, occasionally with one of the actines shorter:

RMNH Por. 8444: 99–118–131 x 11–13.2–15
Combined size data: 72–131 x 7–15 μm

Apical actines (Rodrigues, Figs 32g; Mayotte, Fig. 34c) of the tetractines smooth, usually straight, slightly shorter and thinner than basal actines.

Actines in five Rodrigues specimens:

RMNH Por. 11612: 46–91–158 x 4–6.7–6.5 μm .
RMNH Por. 11660: 24–62–96 x 3–6.3–8 μm
RMNH Por. 11667: 51–73–91 x 5–6.2–7.5 μm
RMNH Por. 11702: 51–85–132 x 5–6.2–8 μm
RMNH Por. 11719: 46–75–108 x 3.5–5.8–7.5 μm

In one Mayotte specimen:

RMNH Por. 8444: 68–82–101 x 5.5–7.1–10 μm .
Combined size data: 24–158 x 3–10 μm

Trichoxeas (Fig. 32e). Most Rodrigues specimens have some fragmented thin diactines, 185–300 x 2–3 μm . Not found in the Mayotte specimen.

Distribution and ecology. Rodrigues, Mayotte, Indonesia, in reefs and on mangrove roots, shallow water, down to 15 m.

Remarks. Morphologically (Figs 31–34) and genetically (Fig. 2B) the Rodrigues and Mayotte specimens match well with the Indonesian specimens. The spicule sizes of the specimens from Indonesia were: triactines 76–107.5–168 x 7.5–9.1–18 μm (averages very similar, upper sizes slightly higher), tetractines, basal actines 84–109.6–153 x 6–8.7–16 μm (ditto), and apical actines 29–82.4–147 x 3–5.3–8 μm (very similar). In the remarks of the description of the Indonesian material (cf. Van Soest & De Voogd 2015) mention is made of trichoxeas, similarly to the present material. The Mayotte specimen falls within the morphological variability of the Rodrigues and Indonesian specimens, although the spicules tend to be more robust and the habitus consists of a series of lobes crowned by oscule-type water-collecting tubes.

To investigate the phylogenetic relationships of the Western Indian Ocean *Ernstia* species we made a separate comparison of sequences of *Ernstia naturalis* with the other partial 28S rRNA sequences of *Ernstia* available to us (Table 1, Fig. 2B). Three Indonesian sequences of *E. naturalis* were available (holotype RMNH Por. 9342, and paratypes 9343 and 5000, obtained subsequently after the description of Van Soest & De Voogd 2015 was published). We obtained seven Rodrigues sequences, as well as a sequence of the *Ernstia naturalis* specimen from Mayotte. We also obtained sequences of Indonesian *Ernstia klautauae* Van Soest & De Voogd, 2015. Oliver Voigt made six sequences of *Ernstia arabica* available to us.

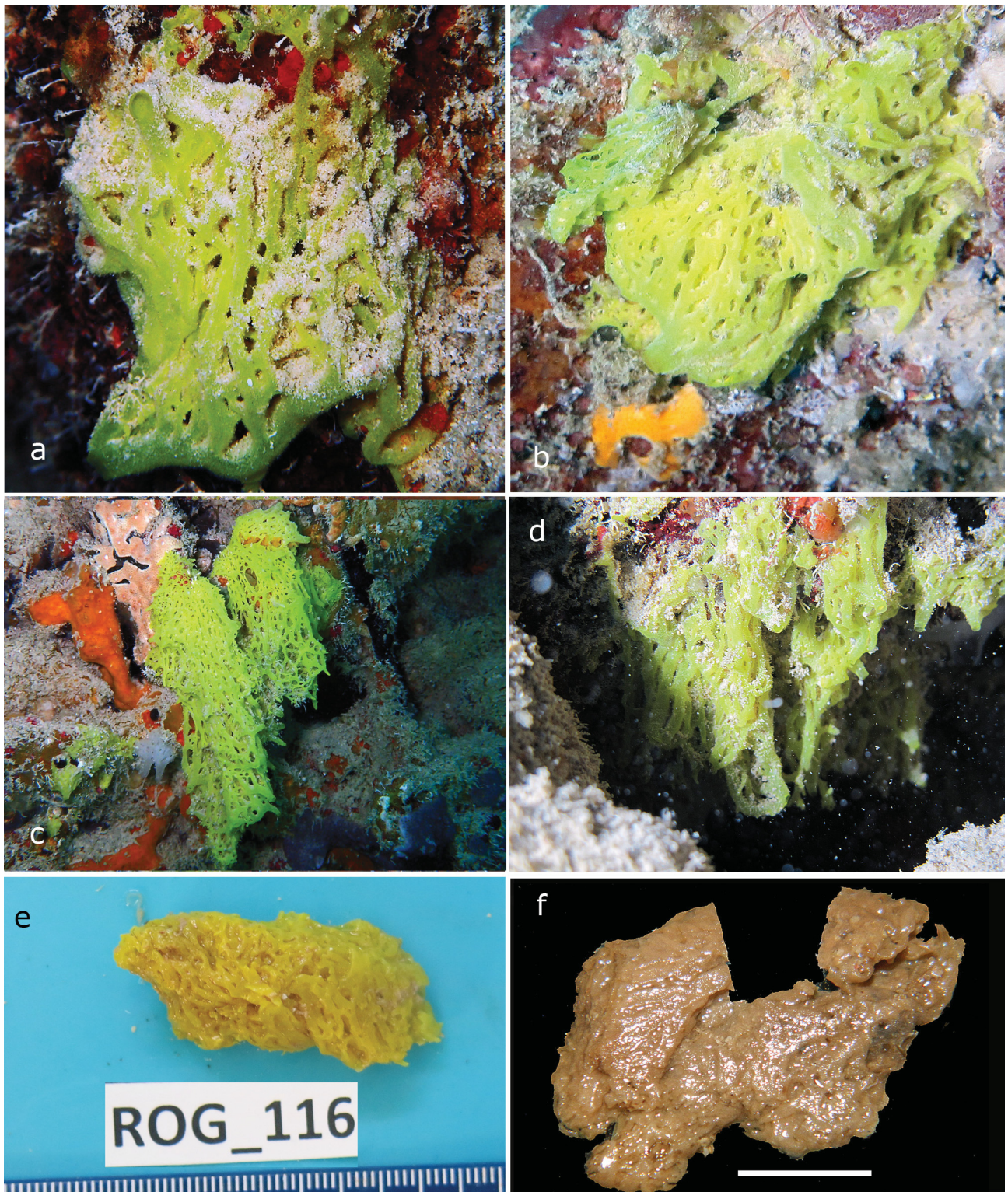


FIGURE 31. *Ernstia naturalis* Van Soest & De Voogd, 2015, a, RMNH Por. 11612 (ROG013), in situ photo from the reef of Rodrigues, b, RMNH Por. 11633 (ROG034), ditto, c, RMNH Por. 11702 (ROG116), d, RMNH Por. 11614 (ROG015), ditto, e, RMNH Por. 11702 (ROG116) on deck photo, f, ditto, photo of preserved specimen (all photos except 34f by N.J. de Voogd).

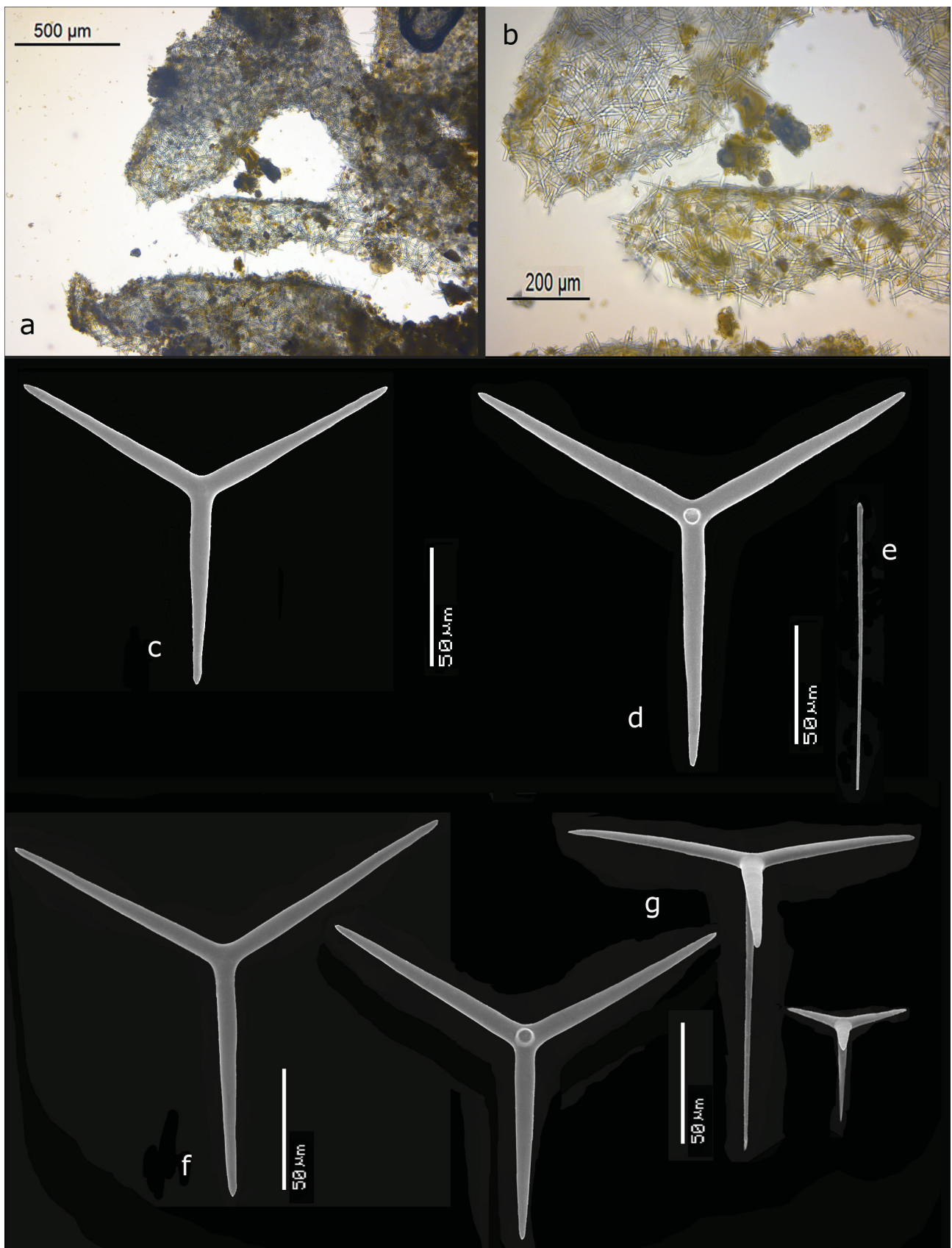


FIGURE 32. *Ernstia naturalis* Van Soest & De Voogd, 2015, a, light microscopic view of cornus of RMNH Por. 11612, b, detail of a, c–g, SEM images of spicules of RMNH Por. 11612 (c–e) and RMNH Por. 11702 (f–g), c,f, triactines, d,g, tetractines, e, fragment of trichoxea.

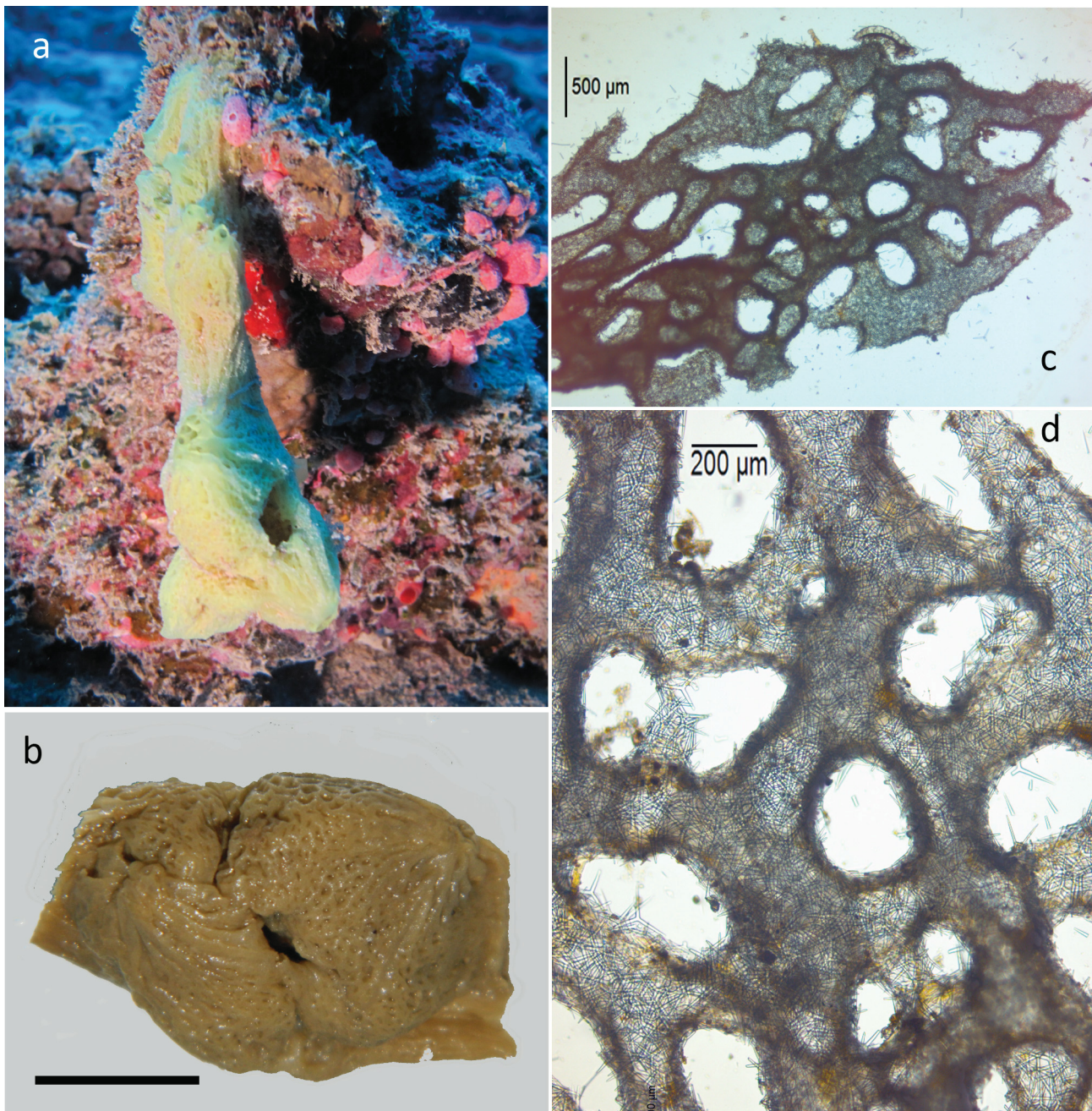


FIGURE 33. *Ernstia naturalis* Van Soest & De Voogd, 2015, RMNH Por 8444 from Mayotte (French Overseas Territory, situated north of Madagascar), a, habitus in situ at Mayotte reef (photo N.J. de Voogd), (b) preserved specimen (scale bar = 1 cm), c–d, light microscopic images of skeleton, c, overview, d, detailed view.

In our sequence analysis, we obtained after trimming an alignment comprising a length of 427 sites. The Indonesian holotype of *E. naturalis* (GenBank acc.nr. MF686063) has two sites difference with seven selected identical sequences from Rodrigues specimens. One of the paratypes (RMNH Por. 5000, GenBank acc.nr. MF686064) has only a single site difference, while the other (RMNH Por. 9343, Gen Bank acc. nr. MF686065)) has four site differences with the Rodrigues specimens. The specimen obtained by us from Mayotte, RMNH Por. 8444 (GenBank acc.nr. MF872757), which showed differences from the holotype of *E. naturalis* in two sites, differed also in four sites from the Rodrigues specimens, thus tending to be closer to the Indonesian representatives. Since all these differences are not consistent and comprise less than 1% of the partial 28S sequences of the 427 sites, we conclude that both the Indonesian, and Rodrigues/Mayotte specimens are assignable to a single species (see also phylogenetic tree of Fig. 2B).

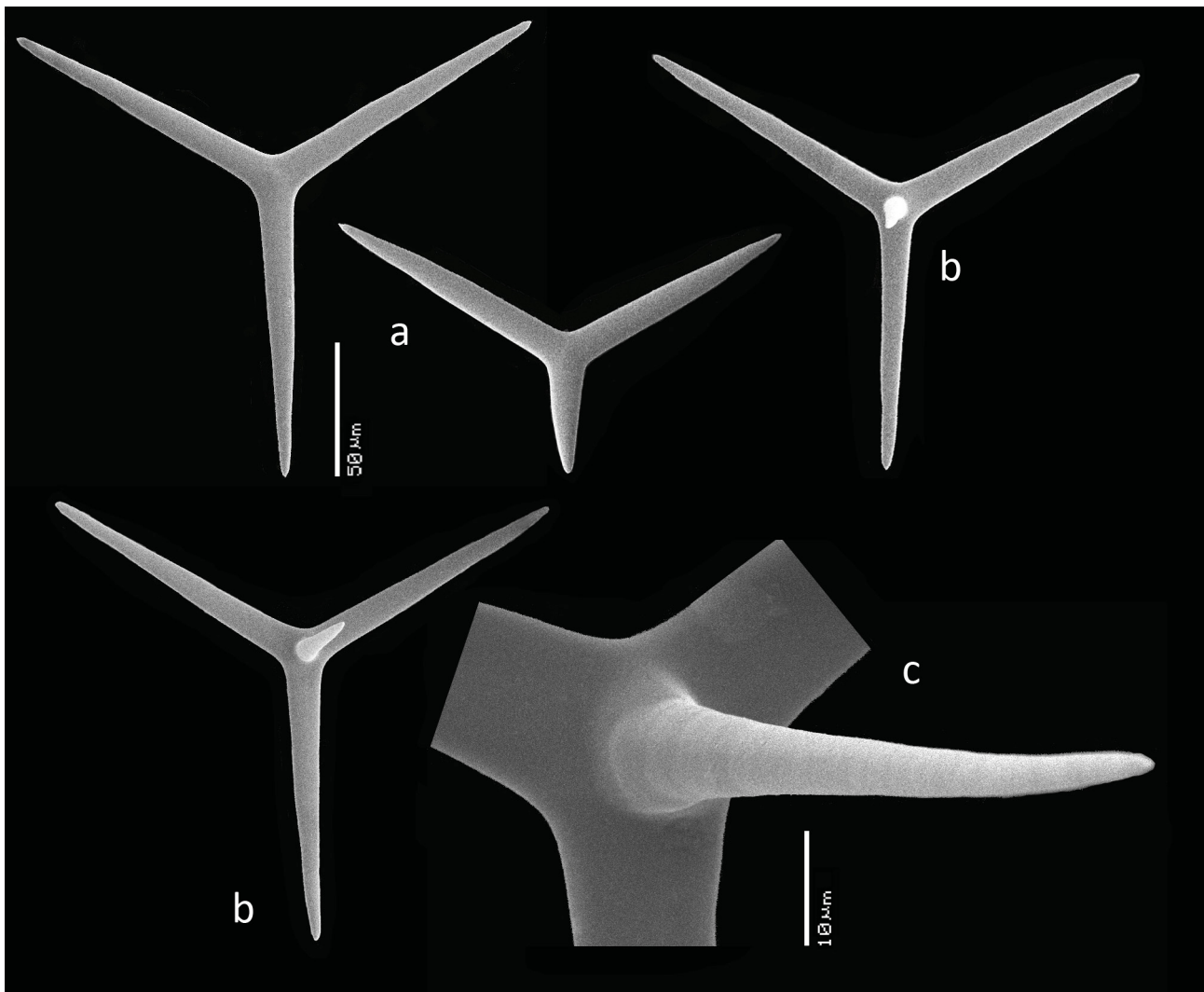


FIGURE 34. *Ernstia naturalis* Van Soest & De Voogd, 2015, RMNH Por 8444 from Mayotte, SEM images of the spicules, a, triactines, b, tetractines, c, detail of apical actine of tetractine.

Indonesian *Ernstia klautauae* Van Soest & De Voogd, 2015 and *Ernstia arabica* Voigt *et al.*, 2017 are close genetically, as they are in a highly supported clade with *E. naturalis* (cf. Fig. 2B). The paratype of *E. klautauae* (RMNH Por. 9341) of which a sequence was available (GenBank acc.nr. MF686062) differed in six sites from the Rodrigues specimens of *E. naturalis*. Six identical *Ernstia arabica* sequences made available to us by Oliver Voigt differed consistently in five sites from the Rodrigues specimens. We conclude that these differences, though small, indicate specific differences, because they are consistent, and they confirm the morphological differences, e.g. tightness of the anastomosed tubuli and the overall smaller size of *E. arabica*.

***Ernstia* aff. *indonesiae* Van Soest & De Voogd, 2015**

Figures 35a–f

? *Ernstia indonesiae* Van Soest & De Voogd, 2015: 21, figs 13a–c, 14a–d, 15a–e.

Material examined. ZMA Por. 11569, Seychelles, SE of Mahé, 4.7833°S 55.5833°E, depth 55 m, trawl, coll. R.W.M. van Soest, field nr. NIOP-E stat. 743/01, 24 December 1992.

Description. Cormus (Fig. 35a) a mass of loosely anastomosed wider and thinner tubuli, size 3 x 1.5 x 1 cm, individual tubuli, 0.3–4 mm in diameter. Color in life whitish, in alcohol transparent-white. Consistency soft to slightly firm.

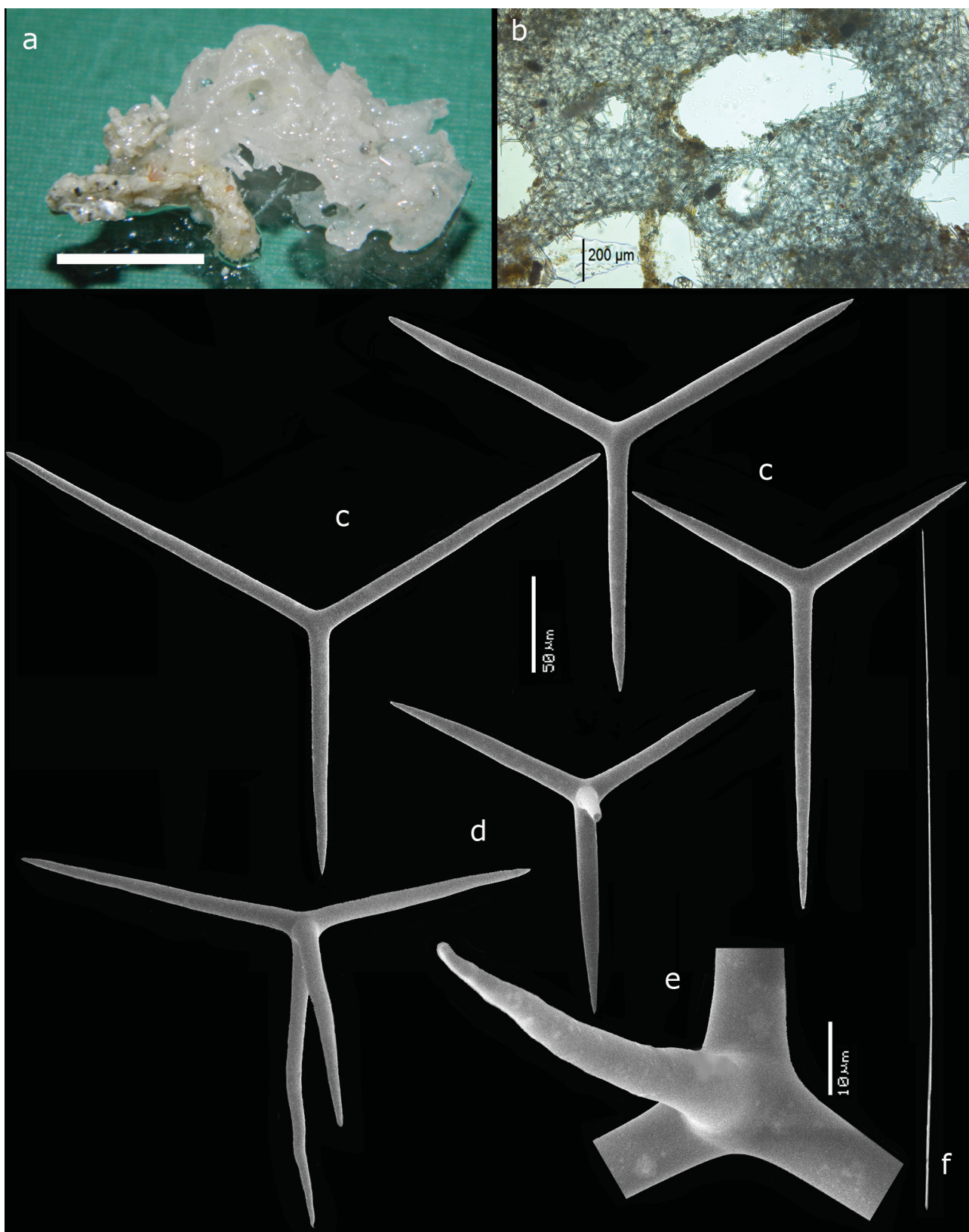


FIGURE 35. *Ernstia* aff. *indonesiae* Van Soest & De Voogd, 2015, ZMA Por. 11569 from the Seychelles, a, preserved specimen (scale bar = 1 cm), b, light microscopic image of the cormus, c–f, SEM images of the spicules, c, triactines, d, tetractines, e, detail of apical actine of tetractine, f, fragment of trichoxea.

Aquiferous system. Asconoid.

Skeleton. (Fig. 35b) Tubule walls consist of two or three layers of triactines and tetractines, with the apical

actines of the latter protruding into the tubular lumina. Infrequent trichoxeas are protruding from the tube walls.

Spicules. (Figs 35c–f) Triactines, tetractines (most common), trichoxeas.

Triactines (Figs 35c) usually equiradial and equiangular, but occasionally slightly sagittal or with actines all three of different length, with cylindrical or cylindroconical actines, 81–159–207 x 8–10.2–12 µm.

Tetractines (Figs 35d), with basal triadial system similar in shape and size to the triactines, with apical actines usually thinner, straight, or slightly curved; actines of basal triadial system 66–153–209 x 7–10.5–13 µm, apical actines (Fig. 35e) 69–108–138 x 5–8.2–10 µm.

Trichoxeas (Fig. 35f), rare, broken pieces only, 130–240 x 1–1.5 µm.

Distribution and ecology. Seychelles, deeper water, possibly Indonesia.

Remarks. By its possession of tri- and tetractines reaching actine sizes to over 200 µm and the presence of thin trichoxeas there is an overall similarity with *E. indonesiae*. However, there are also differences, such as the pinkish life color and yellowish color in alcohol of that species. Spicules are also on average longer and thicker, over 210 x 17 µm. Together these differences are sufficient to differentiate the Indonesian material from the present. Affinity is also present with Sri Lankan and Indonesian *Arturia tenuipilosa* (Dendy, 1905), but that species has the spicules overall smaller, it has a minority of tetractines unlike our specimen, and the trichoxeas are much more frequent.

Unfortunately, our attempts to obtain 28S rRNA sequences failed.

Ernstia spec.

Figures 36a–e

Material examined. RMNH Por. 10161c, Maldives, Faafu Atoll, Wallstreet, 3.119°N 72.979556°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. MAD10/MAS 122, 20 February 2015.

Description. Tiny clump of anastomosed thin tubuli (Fig. 36a, arrow) on a keratose sponge (along with *Clathrina repens* sp.nov.). Overall size 0.4 x 0.3 x 0.15 mm, individual tubuli 0.2–0.5 mm. No visible oscules or water-collecting tubes. Color pink in situ, white in alcohol. Consistency soft.

Aquiferous system. Asconoid.

Skeleton. (Fig. 36b) The tubule walls have two or three layers of triactines and tetractines. Apical actines of the latter protruding in the tubuli lumen.

Spicules. (Figs 36c–e) Triactines and tetractines, in approximately equal proportion.

Triactines (Fig. 36c). Predominantly equiradial and equiangular, but slightly sagittal forms are not uncommon. Actines conical with sharp points, 68–103–128 x 9–12.1–16 µm.

Tetractines (Fig. 36d). Basal triradial system similar in shape and size to triactines, apical actines shorter and thinner. Actines of basal triradial system 46–96–129 x 6–11.1–14.5 µm, apical actines (Fig. 36e) 39–64–96 x 5–7.6–9 µm.

Distribution and ecology. Maldives, reef at 10 m.

Remarks. The material is insufficient to properly characterize a new species, but it is possibly undescribed. *Ernstia arabica* and *Ernstia naturalis* as described above differ clearly in color and in having the tubuli much tighter (*arabica*) or much wider (*naturalis*) anastomosed. As we did not obtain sequence data, for the time being this small specimen has to remain unnamed.

Family Leucaltidae Dendy & Row, 1913

Genus *Leucaltis* Haeckel, 1872

***Leucaltis nodusgordii* (Poléjaeff, 1883)**

Figures 37a–e, 38a–f.

Heteropegma nodusgordii Poléjaeff, 1883 (in part, only the Torres Strait material): 45, pl. I fig. 7, pl. IV figs 1a–d.

Leucaltis clathria; Dendy 1913: 16, pl. I figs 1–2; Hôzawa 1940: 136, pl. VI fig. 3; Wörheide & Hooper 1999: 876, figs 7I–S (not: Haeckel 1872).

Leucaltis nodusgordii; Van Soest & De Voogd 2015: 39, figs 28a–c, 29a–d, 30a–e (with further synonyms).

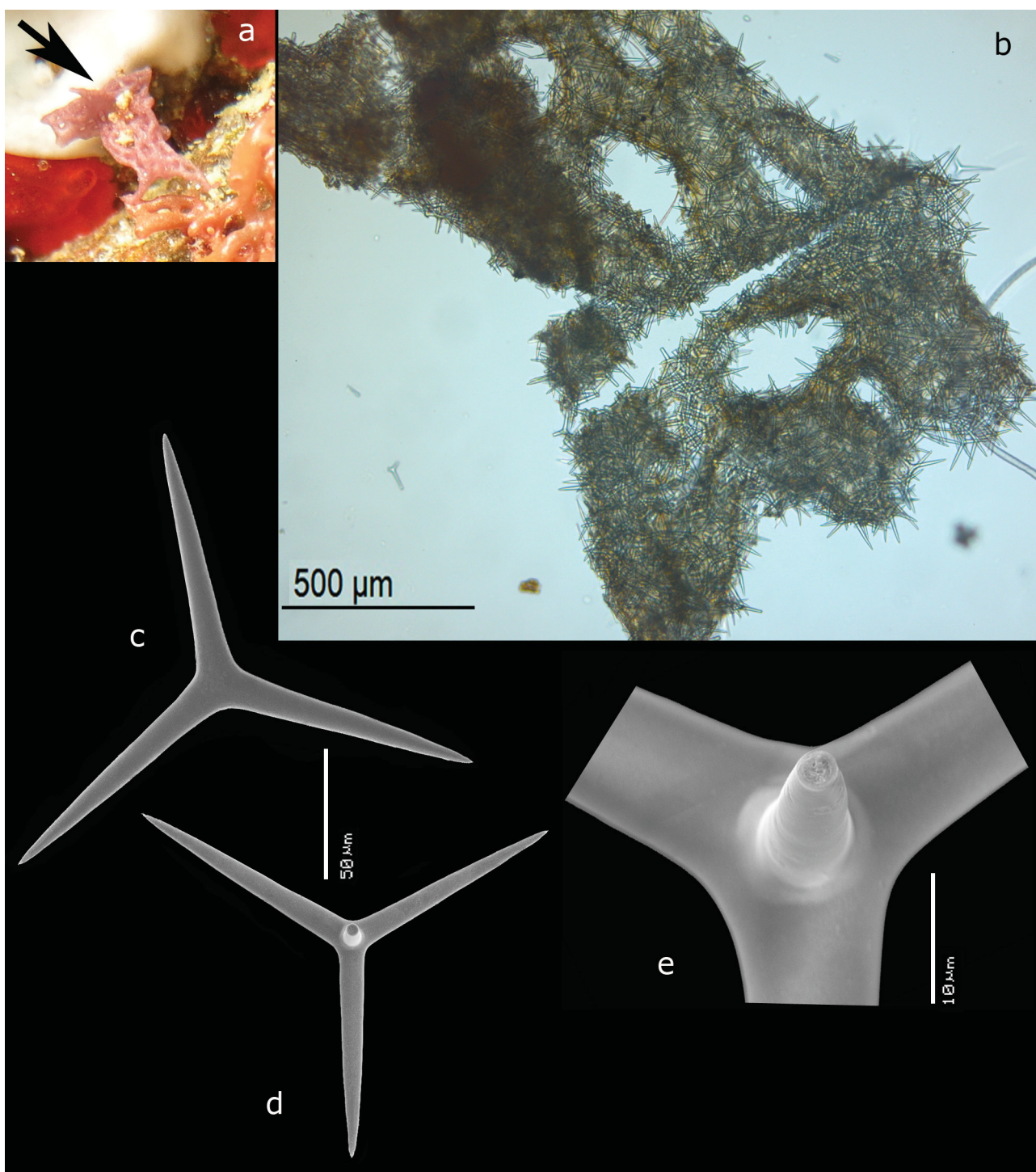


FIGURE 36. *Ernstia* spec., RMNH Por. 10161c, from the Maldives, a, habitus in situ (arrow), b, light microscopic overview of the cornus, c–e, SEM images of the spicules, c, triactines, d, tetractine, e, detail of apical actine of tetractine.

Material examined. ZMA Por. 12436, Seychelles, Amirantes, Desroches Atoll, SW rim, outer reef slope, 5.7167°S 53.6167°E, depth 5–30 m, scuba, coll. M.J. de Kluijver, field nr. NIOP-E stat. 774/03, 30 December 1992; ZMA Por. 12443, Seychelles, Amirantes, Poivre Atoll, N rim, outer reef slope, 5.7333°S 53.3167°E, depth 7–8 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 768/08, 31 December 1992; ZMA Por. 16248, Seychelles, Mahé, SE coast, Anse Royale Bay, 4.7333°S 55.5167°E, depth 2–13 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 740/04, 24 December 1992; ZMA Por. 20623, Seychelles, Mahé, NE Point, 4.5833°S 55.4667°E, depth 0–5 m, snorkling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 604, 8 December 1992.

Description. Because this species has been treated recently in Van Soest & De Voogd (2015), we refrain from

extensively describing the Seychelles material. The species forms masses of loosely anastomosed tubes (Fig. 37a), size up to 3 x 4 cm, individual tubes approximately 0.5 cm in diameter. Color pale blue or bluish white in situ, white in preservation. Some of the tubes have open endings, presumably oscules. Consistency fragile, surface optically smooth, but feels rough.

Aquiferous system. Elongate, ramified choanocyte chambers, supported by small equiangular spicules.

Skeleton. (Figs 37–e) In cross section (Fig. 37b) from outside to atrium, there is a cortical skeleton of giant tri- and tetractines (Fig. 37c), a choanosomal skeleton (Fig. 37d) of small thin equiangular and equiradiate tri- and tetractines, and an atrial membrane (Fig. 37e) supported by small sagittal ('abruptly'-angled) tri- and tetractines.

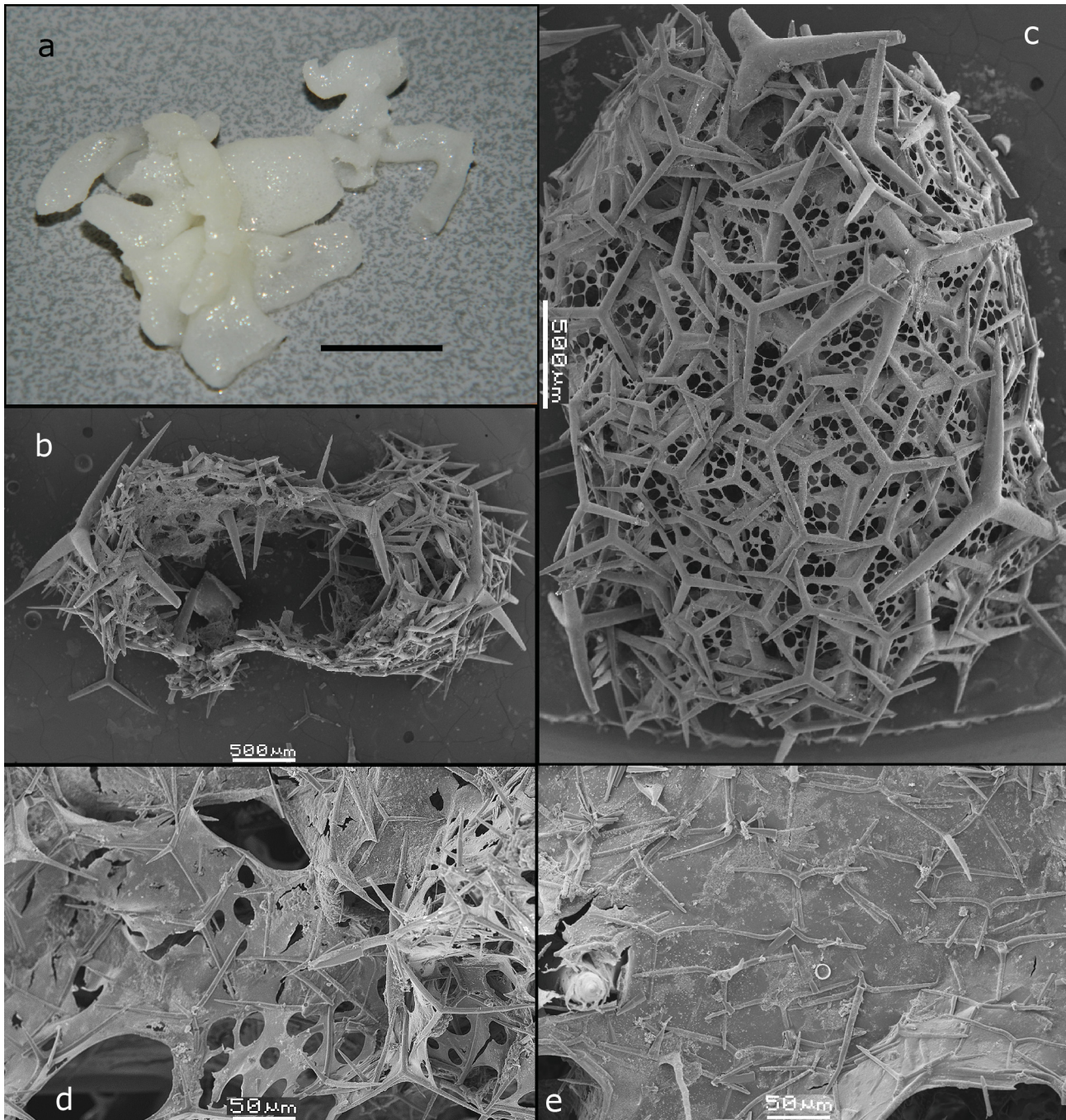


FIGURE 37. *Leucaltis nodusgordii* (Poléjaeff, 1883), ZMA Por. 16248, from the Seychelles, a, preserved habitus (scale bar = 1 cm), b–e, SEM images of the skeleton, b, cross section of tube, c, surface of the tube showing cortex of giant tri- and tetractines, d, part of the choanosomal skeleton showing small regular tri- and tetractines, e, atrial skeleton of sagittal 'abruptly' angled tri- and tetractines.

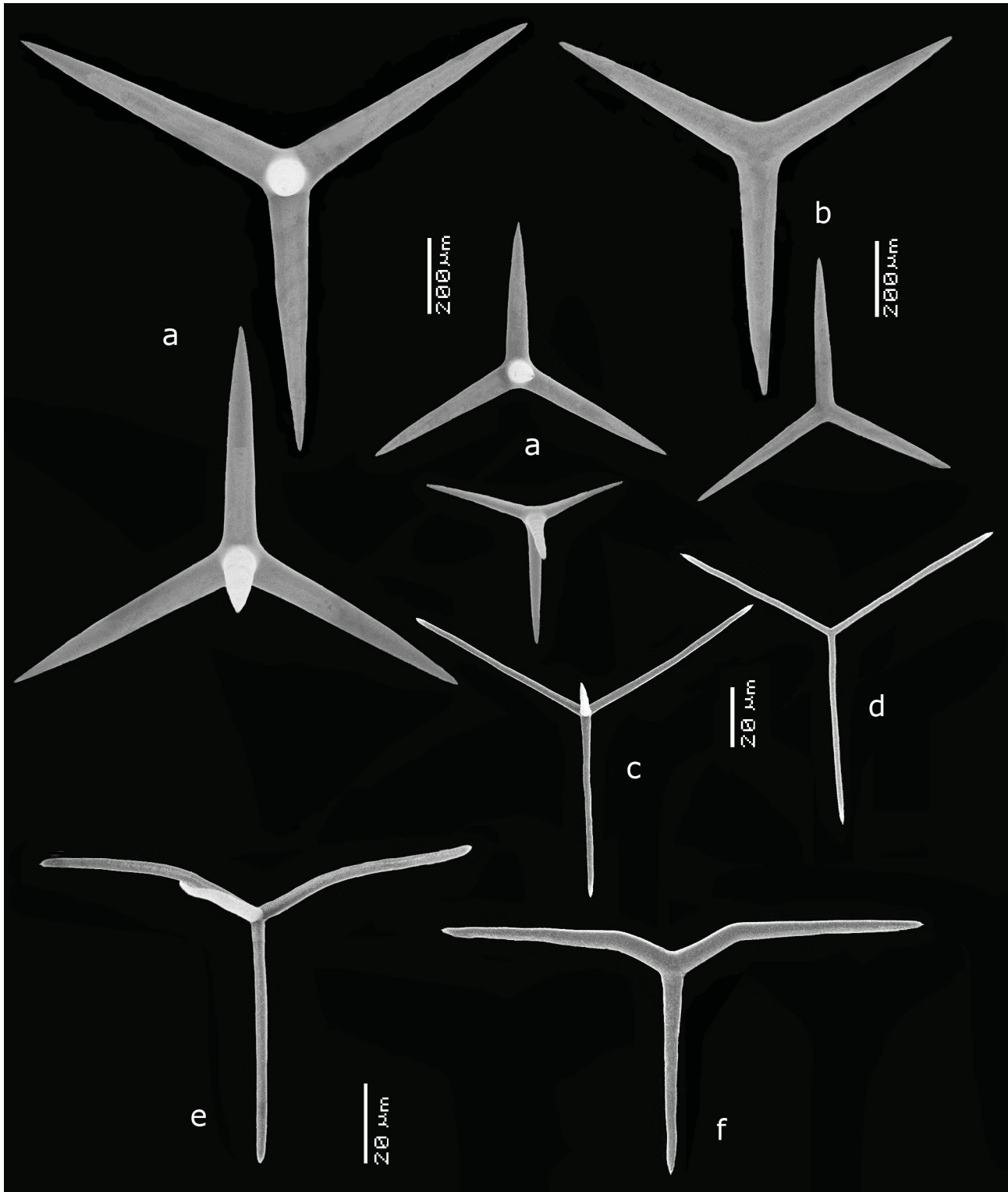


FIGURE 38. *Leucaltis nodusgordii* (Poléjaeff, 1883), ZMA Por. 16248, from the Seychelles, a–f, SEM images of the spicules, a, cortical giant tetractines, b, cortical giant triactines, c, choanosomal regular tetractine, d, choanosomal regular triactine, e, atrial sagittal ‘abruptly’ angled tetractine, f, atrial sagittal ‘abruptly’ angled triactine.

Spicules. (Figs 38a–f) Giant tri- and tetractines, small regular tri- and tetractines, small sagittal tri- and tetractines.

Giant tetractines (Figs 38a), quite variable in size, similar in shape and size to the giant triactines, actines 144–571–1020 x 18–79.8–126 μm.

Giant triactines (Figs 38b), quite variable in size, equiangular and equiradiate, with thick conical actines measuring 102–505–960 x 14–60.2–138 μ m.

Regular equiangular equiradiate tetractines (Fig. 38c), with thin cylindrical actines; basal radiate actines 60–73–84 x 2–2.4–4 μ m, with apical actines 9–20.7–28 x 2–2.1–3 μ m.

Regular equiangular equiradiate triactines (Fig. 38d), with thin cylindrical actines measuring 59–66.9–78 x 2–2.1–3 μ m.

Sagittal, abruptly angled tetractines (Fig. 38e), with unpaired actines 39–57–69 x 2.5–3.5–5 μ m, paired actines 60–69–84 x 2–3.4–5 μ m, apical actines 18–29.8–45 x 2–2.9–5 μ m.

Sagittal, abruptly angled triactines (Fig. 38f), similar to the sagittal tetractines, with unpaired actines 36–50–63 x 2–2.8–4.5 μ m, paired actines 54–64–81 x 2–3.1–4.5 μ m.

Distribution and ecology. Seychelles, Cargados Carajos, Australia, Sri Lanka, Indonesia, on reefs at depths down to 88 m.

Remarks. The data for the Seychelles specimens closely conform to those of the Indonesian material described by us recently. Size of the Seychelles specimens is smaller than the Indonesian ones, but individual tubes are similar in both. The giant tetractines of the Indonesian specimens were reported as somewhat larger. Unfortunately, Dendy's (1905) record of this species from Sri Lanka was not described, so we do not know whether this inbetween locality had inbetween sizes.

We obtained sequences of an Indonesian specimen described in our 2015 paper (RMNH Por. 1772) and two of the Seychelles specimen (ZMA Por. 12436 and 12443) treated here. We also downloaded longer 28S sequences from GenBank of a Panamanian (Caribbean) *Leucaltis* sp. = *L. clathria* (Haeckel, 1872), proclaimed a different species by us (Van Soest & De Voogd, 2015; Van Soest, 2017), and two Australian sequences named *L. clathria* (Haeckel, 1872) (acc.nrs. JQ272302 and AY563542), which are assumed to be conspecific with Indonesian and Seychelles specimens of *L. nodusgordii*. As the detailed relationships between these specimens are not clearly apparent in Fig. 2B, we did a separate analysis of the aligned and trimmed sequences of these six specimens (alignment length 369 sites), which showed 21 non-conserved sites. Where the maximum site difference between the five sequences from the Indo-West Pacific was 6 or less, the Panamanian sequence had 11 unique non-conserved sites, along with two non-conserved sites shared with Indonesia and one with Australia. This supports the previously claimed separate specific status of the Caribbean *Leucaltis* populations, even though the differences among the specimens are not significant enough to show up in the phylogenetic analysis of our Fig. 2B.

A possible junior synonym of *Leucaltis nodusgordii* is *Leucaltis bathybia* var. *mascarenica* Ridley, 1884, reported from the Amirantes, very near to two of our collected specimens (ZMA Por. 12436 and 12443). Ridley's description of the habit and the large tetractines sounds close to our material, but there is not sufficient information to be certain. *Leucaltis bathybia* Haeckel, 1872 from 600 m depth in the Red Sea is not conspecific judging from its description (see also below). It is assigned to *Leucandra* at present (see Van Soest *et al.* 2018), but the predominance of large tetractines makes it more likely that it belongs to *Leucilla*. *L. bathybia* was associated with *Sycettusa* (Calcaronea, Heteropiidae) by Burton (1963, p. 318) but this cannot be accepted.

Genus *Leuclathrina* Borojević & Boury-Esnault, 1987

Leuclathrina translucida Voigt *et al.*, 2018

Figures 39a–f, 40a–c

Leuclathrina translucida Voigt *et al.*, 2018: 151, figs 2A–I, 3A–F.

Material examined. RMNH Por. 10072, Maldives, Faafu Atoll, Wallino, 3.087472°N 72.9567°E, depth 20 m, scuba, coll. N.J. de Voogd, field nr. MAD02/MAS022, 16 February 2015; RMNH Por. 10090, Maldives, Faafu Atoll, Coral Garden, 3.0875°N 72.968861°E, depth 18 m, scuba, coll. N.J. de Voogd, field nr. MAD04/MAS043, 17 February 2015.

Description. In life, these sponges form pale yellow cushions (Figs 39a–b, e) consisting of dense layers of anastomosed thin tubes, from which issue long upright tubes. These long tubes are yellow at the base, but become transparent towards their ends (Figs 39a–b). The ends may be broadly flattened or occasionally bifid or curling

downwards. The tubes are mostly closed but some are open and may function as oscules. The yellow base is ‘punctate’, i.e. there are regularly spaced rounded openings separating the tubes. On deck photos (Figs 39c,f) show the specimens to become uniformly yellow, while preserved specimens (3 in RMNH 10072, 1 in RMNH 10090) become pale orange-brown all over (Fig. 39d). The size of preserved specimens is up to 4 x 3 x 1 cm, length of upright tubes 1–2 cm, width 3–4 mm, but the preservation has caused notable shrinkage, so in situ sizes are larger.

Aquiferous system. Leuconoid, not supported by spicules.

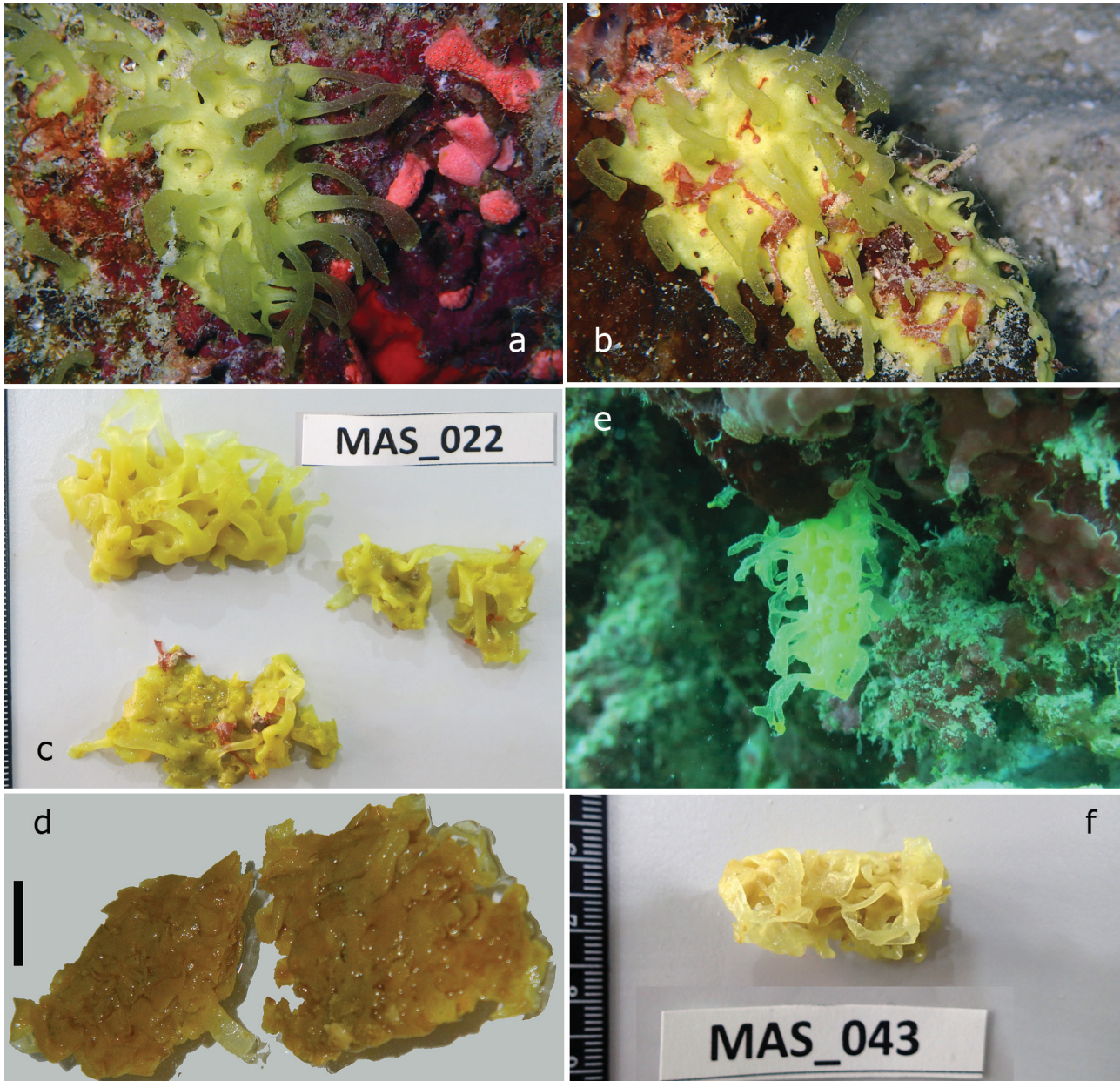


FIGURE 39. *Leuclathrina translucida* Voigt *et al.*, 2018, RMNH Por. 10072 and 10090 from the Maldives, habitus in situ, on deck and preserved, a–b, habitus in situ of RMNH Por. 10072, c, habitus on deck of RMNH Por. 10072 (both photos N.J. de Voogd), d, preserved habitus of RMNH Por. 10072 (scale bar = 1 cm), e, habitus in situ of RMNH Por. 10090, f, habitus on deck of RMNH Por. 10090 (both photos N.J. de Voogd).

Skeleton. (Figs 40a,b) Thickness of tube walls consisting of two layers of overlapping triactines, or more than two layers in the upright long tubes. Insides of the bottom layer tubes and the basal parts of the long upright tubes (Fig. 40b) covered in yellow-colored organic mass, devoid of spicules, presumed to be choanoderm. The extent and thickness of this choanoderm precludes the tubes to be asconoid. This organic layer is absent from the end of the long tubes coinciding with the transparent parts observed in situ.

Spicules. (Figs 40c) Triactines only.

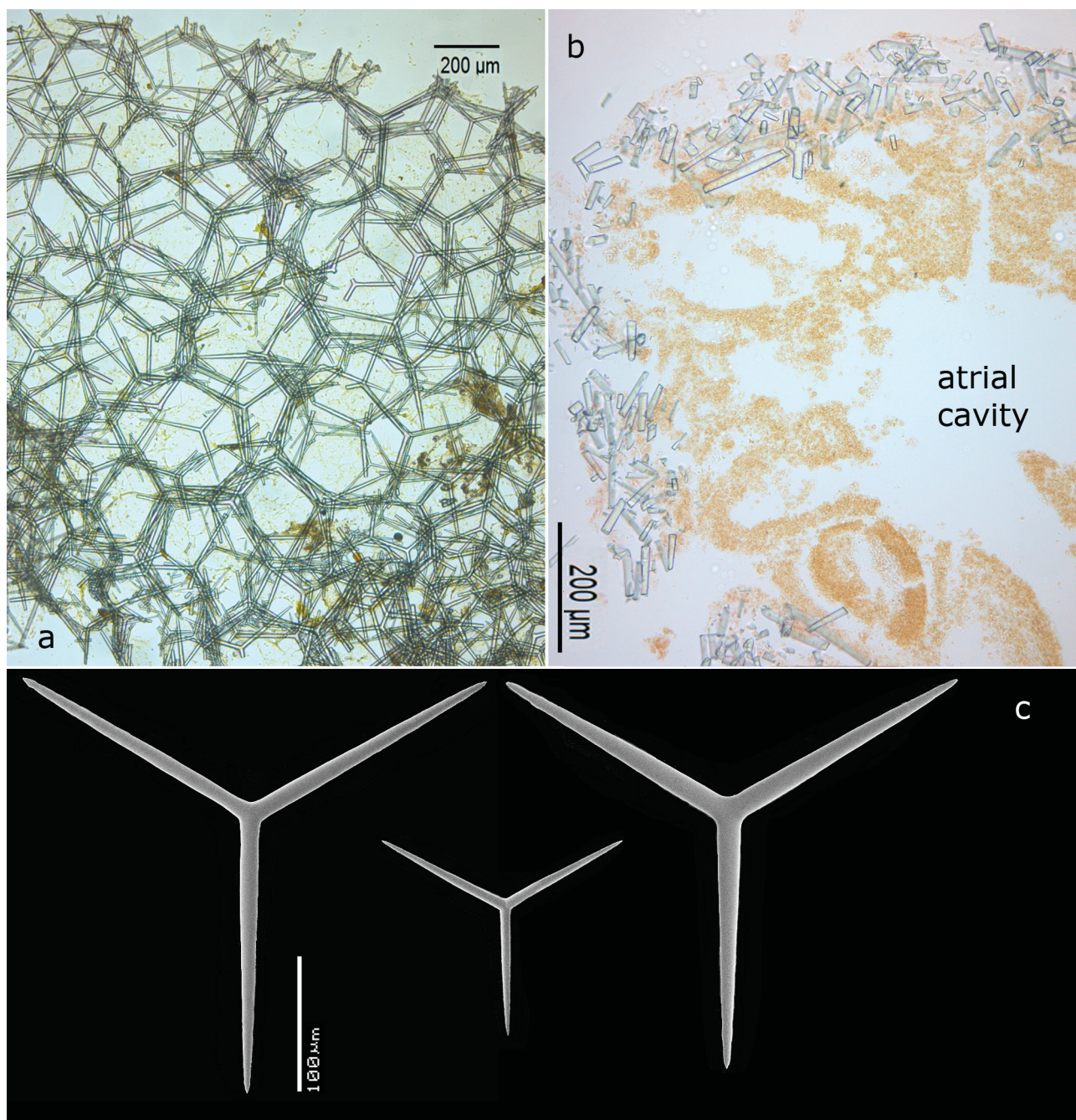


FIGURE 40. *Leuclathrina translucida* Voigt *et al.*, 2018, RMNH Por. 10072, from the Maldives, a, light microscopic image of surface skeleton, b, light microscopic image of a longitudinal cross section of a tube, showing surface cover of spicules and choanosomal soft parts, c, SEM images of the spicules.

Triactines, equiradiate and equiangular, in a large size range, 101–181–243 x 8–13.1–19 µm (RMNH Por. 10072: 101–238 x 8–19 µm, RMNH Por. 10090: 122–243 x 10–15 µm).

Distribution and ecology. Maldives, coral reefs

Remarks. This is a peculiar and deviating Clathrinida, assigned to *Leuclathrina* by Voigt *et al.* (2018) because of the presence of uniformly sized triactines at the surface with a choanoderm not supported by spicules. The 28S sequence we obtained (GenBank acc.nr. MF872789) grouped with Oliver Voigt's sequence (nr. GW393) with 99% bootstrap value confirming the specimens belong to the same species. Because the affiliation of this species is rather uncertain, we included in our phylogenetic tree several sequences of possible close relatives (*Burtonulla*, *Ascandra*, *Levinella* and *Soleneiscus*). Although *Leuclathrina translucida* appeared indeed in the same clade as these genera (cf. Fig. 2B), the bootstrap value is low, so none of the mentioned genera is likely close.

In the process, we made the discovery that the Indonesian *Ernstia chrysops* Van Soest & De Voogd, 2015 is apparently not an *Ernstia* but more likely an *Ascandra*.

So far, the position of *Leuclathrina translucida* in the molecular tree of Fig. 2 is outside and independent of the clades of *Clathrina*, *Leucaltis*, *Ernstia* and *Leucetta*. *Ascandra* species may have a rather similar habitus, but they have a majority and diversity of tetractines. Previously, *Leuclathrina* was monospecific and occurred in bathyal coral reefs off the coasts of Northwestern Europe. This second species is unlike the type species in shape, color and habitat.

Family Leucascidae Dendy, 1892

Genus Leucascus Dendy, 1892

Leucascus schleyeri sp.nov.

Figures 41a–g, 42a–h

? *Clathrina reticulum*; Borojević 1967: 189, fig. 2 (not: Schmidt 1862).

Clathrina aff. *reticulum*; Rudi *et al.* 2000: 1434.

Material examined. Holotype, ZMA Por. 15734, South Africa, Kwazulu Natal, Sodwana Bay, 27.55°S 32.6833°E, coral reef, depth 22–27m, scuba, coll. M. Schleyer, field nr. TASA53-S52, year 2000, undated.

Description. Massive lobate cormus (Fig. 41a), consisting of densely and tightly anastomosed tubuli, with oscules on top of the lobes leading to atrial spaces. Color pink in situ. Preserved material consists of two fragments, each 2 x 2 x 1 cm of the much larger specimen, estimated to be 6 x 4 x 2 cm, most of which was used for natural products research. The preserved fragments are white or cream colored (Fig. 41b) and comprise several contracted lobes.

Aquiferous system. Asconoid, limited to the anastomosed tubuli.

Skeleton. In cross section (Figs 41c–d) the skeleton shows the dense arrangement of contracted tubuli of 0.1–0.2 mm in diameter surrounding shallow atria (Fig. 41d). The atrial walls are separated from the walls of the tubuli by their own layer of tri- and tetractines, as is visible in some parts of Figs 41c–d. There is a cortical surface layer (Figs 41e–f) recognizable by the presence of erect banana-shaped diactines, detailed also in Figs 15c–d. The walls of the tubuli are built by several layers of triactines and tetractines. The latter protrude with their apical actines into the tubule lumen (Fig. 42a). We noticed the presence of parasitic or commensal copepods in the cormus (Fig. 42b).

Spicules. (Figs 42e–h) Triactines and tetractines, the latter with spined apical actines.

Triactines (Fig. 42e) equiradial and equiangular, with cylindroconical actines measuring 54–74.6–90 x 4.5–6.7–8.5 µm.

Tetractines (Figs 42f–g) similar in shape and size to the triactines, occasionally somewhat sagittal, with thin straight apical actines provided with three rows of strong spines the position of which is matching the basal triradial system (Figs 42g), actines of the basal triradial system 63–78–91 x 5–6.5–8.5 µm, apical actines 31–49–76 x 2–4.4–7 µm.

Diactines, asymmetrical, curved, ‘banana’-shaped, often eroded (probably artefactual) and grooved, 48–76–98 x 8–9.6–12 µm.

Distribution and ecology. Natal coast of South Africa, deep reef.

Etymology. Named after Dr Michael Schleyer, Oceanographic Research Institute, Durban, South Africa, who collected the material, and in recognition of his important work on the marine ecology of South Africa.

Remarks. Although we do not have molecular sequence data for this specimen, the overall similarity of the present material with *Leucascus*, reviewed by Cavalcanti *et al.* (2003), makes it likely that the present new species is also a member of that genus. Our SEM cross sections (Figs 41c–d) show the characteristic structure of short atrial cavities surrounded by tightly anastomosed tubuli, with the whole cormus covered with a cortex of erect short diactines. Of the described species of *Leucascus*, only South Australian *L. clavatus* Dendy, 1892 possesses diactines, but these are much larger and thicker (350–850 x 99–140 µm) than those of the new species, while also the tri- and tetractines are significantly larger (actines 70–160 x 9–19 µm).

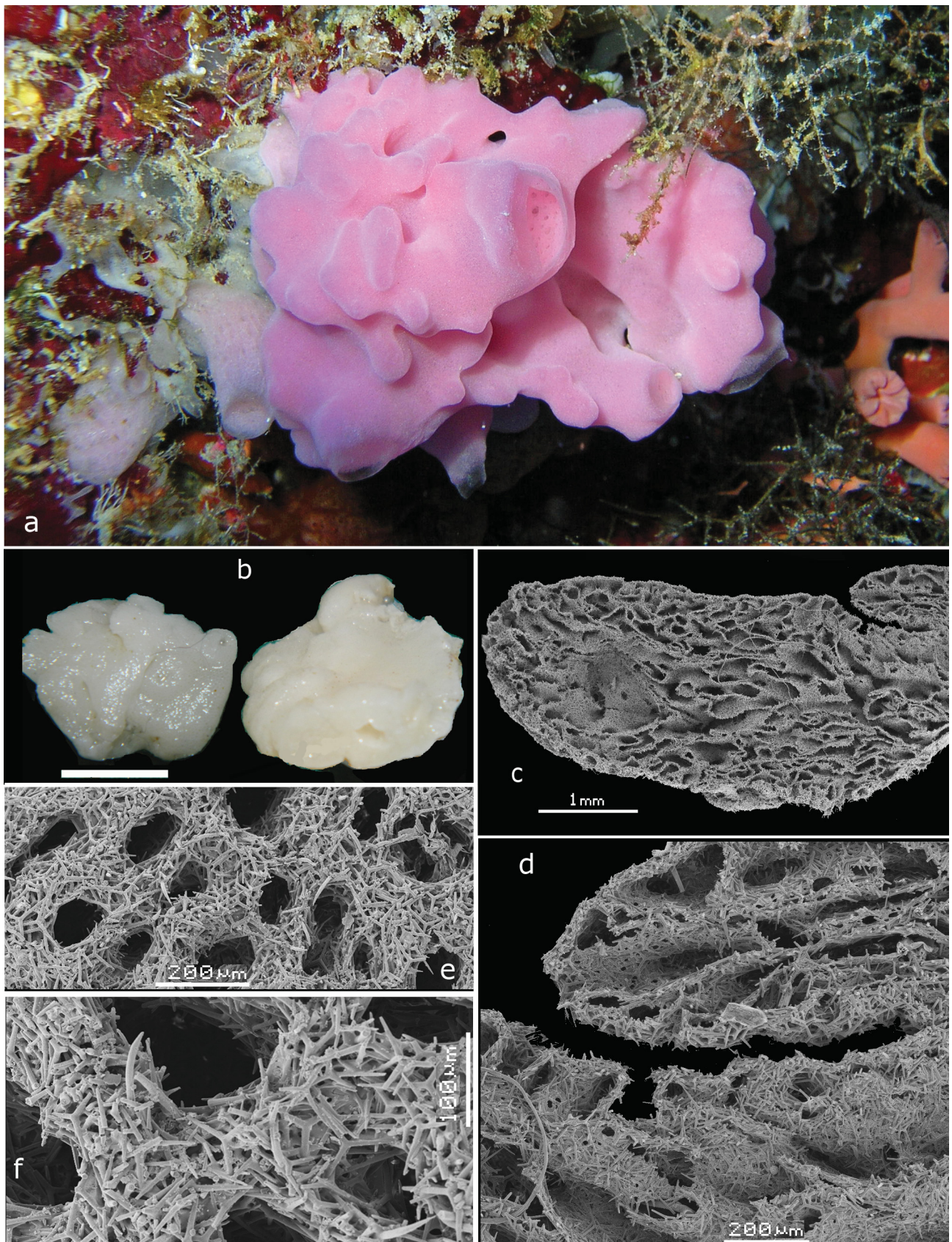


FIGURE 41. *Leucascus schleyeri* sp.nov., holotype ZMA Por. 15734, a, habitus in situ on the deep reef of Sodwana Bay, Kwazulu Natal, South Africa (photo M. Schleyer), b, preserved fragments of holotype (scale bar = 1 cm), c, SEM image of cross section of cormus showing dense mass of tubuli, d, detail of c showing shallow pseudoatrium, e, SEM image of overview of surface, f, detail of e showing erect diactines.

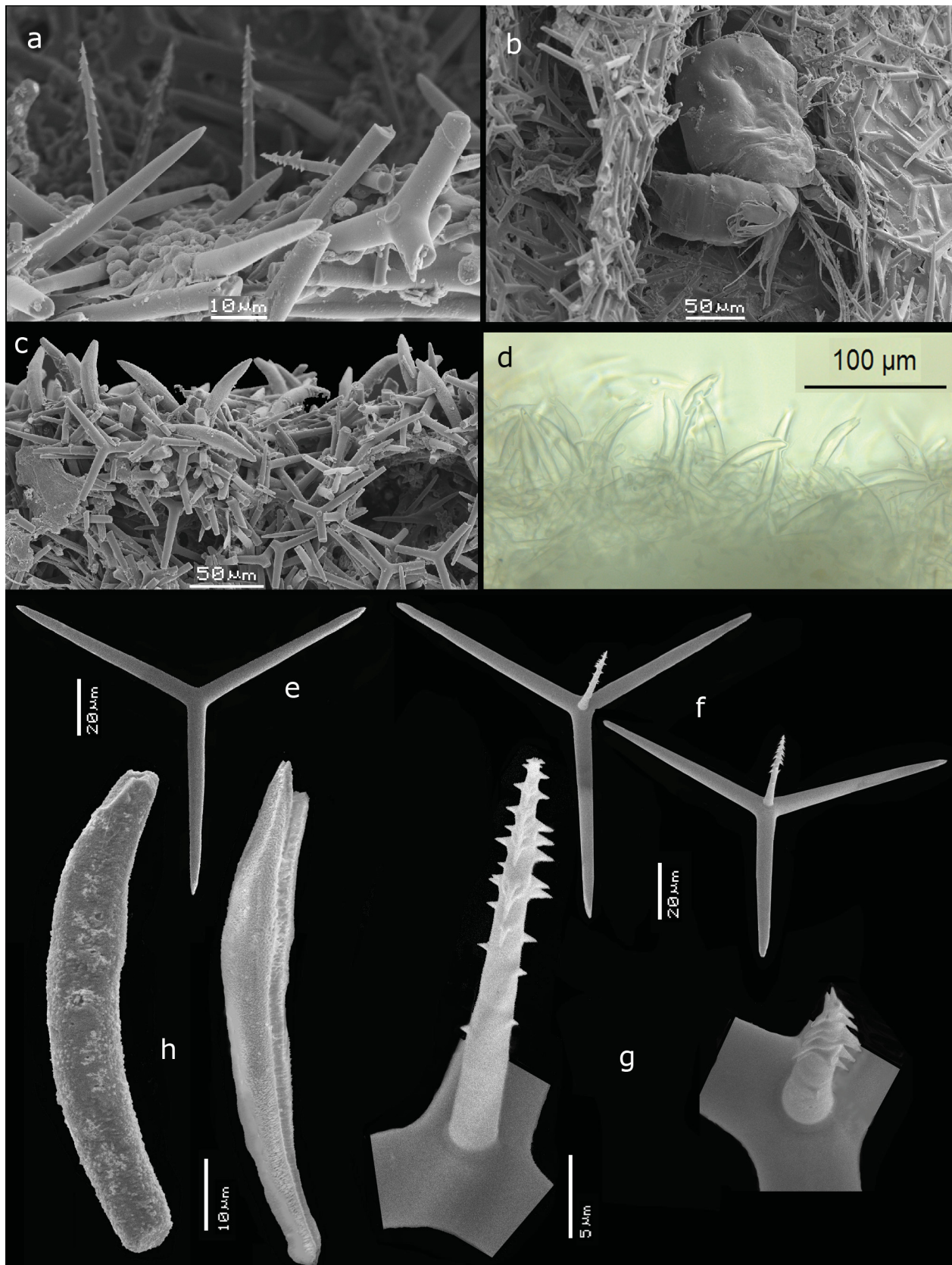


FIGURE 42. *Leucascus schleyeri* sp. nov., holotype ZMA Por. 15734, a, SEM image of wall of tubulus with protruding apical actines of tetractines, b, SEM image of parasitic or commensal copepods lodged in the cornus, c, SEM image of perpendicular section of the upper surface showing crowded 'banana'-shaped erect diactines, d, light microscopic image of the same, e–h, SEM images of spicules, e, triactine, f, tetractines, g, details of apical actines of tetractines, h, 'banana'-shaped diactines from the upper surface.

Borojević (1967) reported *Ascaltis reticulum* (Schmidt, 1862) (as *Clathrina*) from South Africa, from both the Indian Ocean coast ('Natal shore') and from the Atlantic coast (False Bay). He gave a general description for these specimens, which fits our material except for the diactines, which measured 100–200 x 15–20 µm, well in excess of our diactines. No mention was made of spines on the apical actines of the tetractines. *A. reticulum* is originally described from the Mediterranean (Schmidt, 1862). It is possible that at least the Natal specimens could be conspecific with our specimen rather than with *A. reticulum*. Klautau *et al.* (2016) redescribed Adriatic *Ascaltis reticulum* (Schmidt, 1862) and provided molecular sequence data. The spicule types and sizes described by Klautau *et al.* conform rather closely to those cited above for our specimen, except for the diactines which were longer and thinner (60–142 x 4–6 µm) and not eroded. Of course, *Ascaltis* differs from *Leucascus* in lacking a lined atrial cavity (Borojević *et al.* 2002a), and generally is less elaborate in shape and structure. Molecular sequence data of *Ascaltis reticulum* provided by Klautau *et al.* (2016), and downloaded from GenBank were found to group at a rather low bootstrap value with sequences of the Indonesian *Leucascus flavus* described by us previously (Van Soest & De Voogd, 2015) in our Calcinea phylogeny (Fig. 2C). This would confirm a close relationship of *Ascaltis* and *Leucascus* as postulated by Borojević *et al.* (2002a). Nevertheless, there are no molecular sequence data available for the type species of *Ascaltis*, *A. lamarcki* (Haeckel, 1872), so the true affiliation of *Leucascus* and *Ascaltis* remains uncertain.

Dendy's (1913) *Leucosolenia gardineri* from the Western Indian Ocean on paper looks close to the present new species, the major obvious difference appearing to be the lack of banana-shaped diactines in *L. gardineri*. The species is currently assigned to *Ascaltis*.

Novel natural products, clathculins A and B, have been described from this specimen by Rudi *et al.* 2000.

Family Leucettidae De Laubenfels, 1936

Genus *Leucetta* Haeckel, 1872

Leucetta chagosensis Dendy, 1913

Figs 43a–f, 44a–g

Leucetta chagosensis Dendy, 1913: 10, pl. 1 fig. 6, pl. 4 fig. 2; Van Soest & De Voogd 2015: 51, figs 37a–f, 38a–d, with further synonyms.

Ascoleucetta sagittata Cavalcanti *et al.*, 2013: 308, figs 21–22; Van Soest & De Voogd 2015: 49, figs 36a–f.

Material examined. RMNH Por. 9171, Saudi Arabia, Al Laith, Quita al Qursh (Shark Reef), 20.1327°N 40.0994°E, depth 7.8–9.1 m, scuba, coll. Diaa Youssef, field nr. KSA-51, 14 May 2013; RMNH Por. 9621, Saudi Arabia, Jeddah, near Thuwal, Al Asoul, 22.265361°N 39.002139°E, coll. N.J. de Voogd, scuba, field nr. THU07/JED116, 9 November 2014; RMNH Por. 9637, Saudi Arabia, Jeddah, near Thuwal, Um Alsawi, 22.239306°N 38.985139°E, coll. N.J. de Voogd, scuba, field nr. THU08/JED137, 11 November 2014; RMNH Por. 9638, Saudi Arabia, Jeddah, near Thuwal, Um Alsawi, 22.239306°N 38.985139°E, coll. N.J. de Voogd, scuba, field nr. JED138, 11 November 2014; RMNH Por. 9676, Saudi Arabia, Jeddah, near Thuwal, Fsar, 22.229611°N 39.029028°E, scuba, coll. N.J. de Voogd, field nr. THU12/JED181, 13 November 2014; RMNH Por. 10073, Maldives, Faafu Atoll, Wallino, 3.087472°N 72.9567°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. MAD02/MAS023, 16 February 2015; RMNH Por. 10114, Maldives, Faafu Atoll, Route 66, 3.07825°N 72.976306°E, depth 20 m, scuba, coll. N.J. de Voogd, field nr. MAD09/MAS069, 20 February 2015; RMNH Por. 10141, Maldives, Faafu Atoll, Sunny Reef, 3.144639°N 73.012667°E, depth 7 m, scuba, coll. N.J. de Voogd, field nr. MAD08/MAS099, 18 February 2015; RMNH Por. 10144, Maldives, Faafu Atoll, Route 66, 3.07825°N 72.976306°E, depth 20 m, scuba, coll. N.J. de Voogd, field nr. MAD09/MAS105, 20 February 2015; RMNH Por. 11601, Mauritius, Rodrigues, La Rampe, 19.65015°S 63.4132333°E, depth 18 m, scuba, coll. N.J. de Voogd, field nr. ROG001, 15 October 2016; RMNH Por. 11656, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG060, 17 October 2016; RMNH Por. 11657, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG061, 17 October 2016; RMNH Por. 11658, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG062, 17 October 2016; ZMA Por. 13480, Israel,

Gulf of Aqaba, Coral Garden, in cave at 1.5 m depth, scuba, coll. M. Wunsch field nr. AQ139, 15 July 1998; ZMA Por. 13624, Israel, Gulf of Aqaba, Shark Observatory, depth 15 m, scuba, coll. M. Wunsch field nr. RM201, 22 July 1998; ZMA Por. 21468, Saudi Arabia, Abu Madai Reef, 22.0609°N 38.7679°E, depth 19 m, scuba, coll. J. On On Lee, field nr. 4–8, 14 April 2009; ZMA Por. 12071, Seychelles, Amirantes, Alphonse Atoll, SE part of lagoon, 7.0333°S 52.7333°E, depth 6–8 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 788/08, 4 January 1993; ZMA Por. 12442, Seychelles, Amirantes, Platte Island Atoll, lagoon, 5.8333°S 55.35°E, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 797, 7 January 1993; ZMA Por. 16369, Madagascar, Nosy Bé, Ambariobé, N of Nosy Komba, reef, depth 6–8 m, scuba, coll. J.H. Stock, 28 December 1963; ZMA Por. 16372, Madagascar, Nosy Bé, S of Nosy Tanga, reef, depth 7–9 m, scuba, coll. J.H. Stock, 1 January 1964; ZMA Por. 19251, India, Lakshadweep, Minicoy, depth 20 m, scuba, coll. A. George IERSE, field nr. 91, 5 December 2004; ZMA Por. 19279, India, Lakshadweep, Kavaratti, depth 22 m, scuba, coll. A. George IERSE, field nr. 20, 19 February 2005.

Description. Because we recently provided an extensive description of Indonesian specimens of this species (cf. Van Soest & De Voogd 2015), we treat it here in summary format. Habitus in situ (Figs 43a–f) is lobate, ovoid or irregularly massive, usually bright yellow in color (dull beige in preservation), with one or several prominent oscules with short rim. The oscule leads to a slit-like or more expanded atrial cavity. Surface optically smooth. Size of specimens up to 11 x 6 x 4 cm, often smaller. Consistency firm to hard.

Aquiferous system. Leuconoid.

Skeleton. (Figs 44a–b) The skeleton is formed by a dense mass of spicules surrounding the choanocyte chambers of the leuconoid aquiferous system. At the surface there are giant triactines in tangential position, numbers variable among individuals. The oscular rims are provided with smaller somewhat sagittal triactines, often with undulate paired actines. The atrial surface contains numerous tetractines, with their apical actines protruding into the atrial cavity.

Spicules. (Figs 44c–g) Giant triactines, smaller triactines, tetractines.

Giant triactines (Fig. 44c) with rather thin, sharply pointed actines, quite variable among the individuals, 480–789–1380 x 36–61.8–114 µm.

Small triactines (Fig. 44d), similarly sharply pointed, 78–153–258 x 6–13.3–23 µm. Sagittal triactines (Fig. 44e) of the oscular rim: 105–123–144 µm x 6–11.1–17 µm.

Tetractines, with size and shape comparable to the small triactines, basal actines 121–141–180 x 8–11.3–16 µm; apical actines, frequently with curved endings, 32–87–170 x 3–7.4–12 µm.

Distribution and ecology. Seychelles, Red Sea, India, Maldives, Madagascar, Rodrigues; elsewhere throughout Indo-West Pacific tropical waters (see Wörheide *et al.* 2008; Van Soest & De Voogd 2015); common on reefs down to 25 m.

Remarks. The actines of the giant triactines in the Western Indian Ocean on average are larger and thicker than those reported for Indonesian specimens (compare with Van Soest & De Voogd's 2015 measurements). However, the smaller spicules are similar in size, so a conclusion that there is a distinct regional difference is not (yet) warranted. We obtained several partial 28S sequences, both from Indonesian and from Rodrigues specimens.

We also obtained a sequence of the Indonesian holotype of *Ascoleucetta sagittata* Cavalcanti *et al.*, 2013. In our phylogenetic tree of Fig. 2C the latter ended up in a larger clade of *Leucetta chagosensis*, closest to Indonesian specimens of that species. In a separate inspection of a trimmed alignment of 396 sites, the sequence of *Ascoleucetta sagittata* was found to be identical to three Indonesian specimens (one additional Indonesian specimen had one site different). The three Indonesian sequences and the *Ascoleucetta sagittata* sequence together differed in 2 sites from Western Indian Ocean specimens obtained from Rodrigues, and in 3 sites from the Maldives sequence of *L. chagosensis*. These results confirm the already suggested synonymy (cf. Van Soest & De Voogd 2015) of *L. chagosensis* and *Ascoleucetta sagittata*.

The differences between sequences from the Western Indian Ocean (excepting the Maldives) and Red Sea sequences obtained from Oliver Voigt showed a consistent single site difference, Indonesian and Red Sea differences amounted to 2 sites.

A sequence of the Australian *Leucetta villosa* Wörheide & Hooper, 1999 downloaded from GenBank was also found to be included in the larger clade of *L. chagosensis* (cf. Fig. 2C). In the separate inspection mentioned above, the sequence of *L. villosa* differed in five/four sites from Indonesian and Western Indian Ocean *L. chagosensis* sequences. Because of the habitus differences (villous surface) this is interpreted as evidence of specific difference, indicating a possible species complex in *L. chagosensis* s.l.

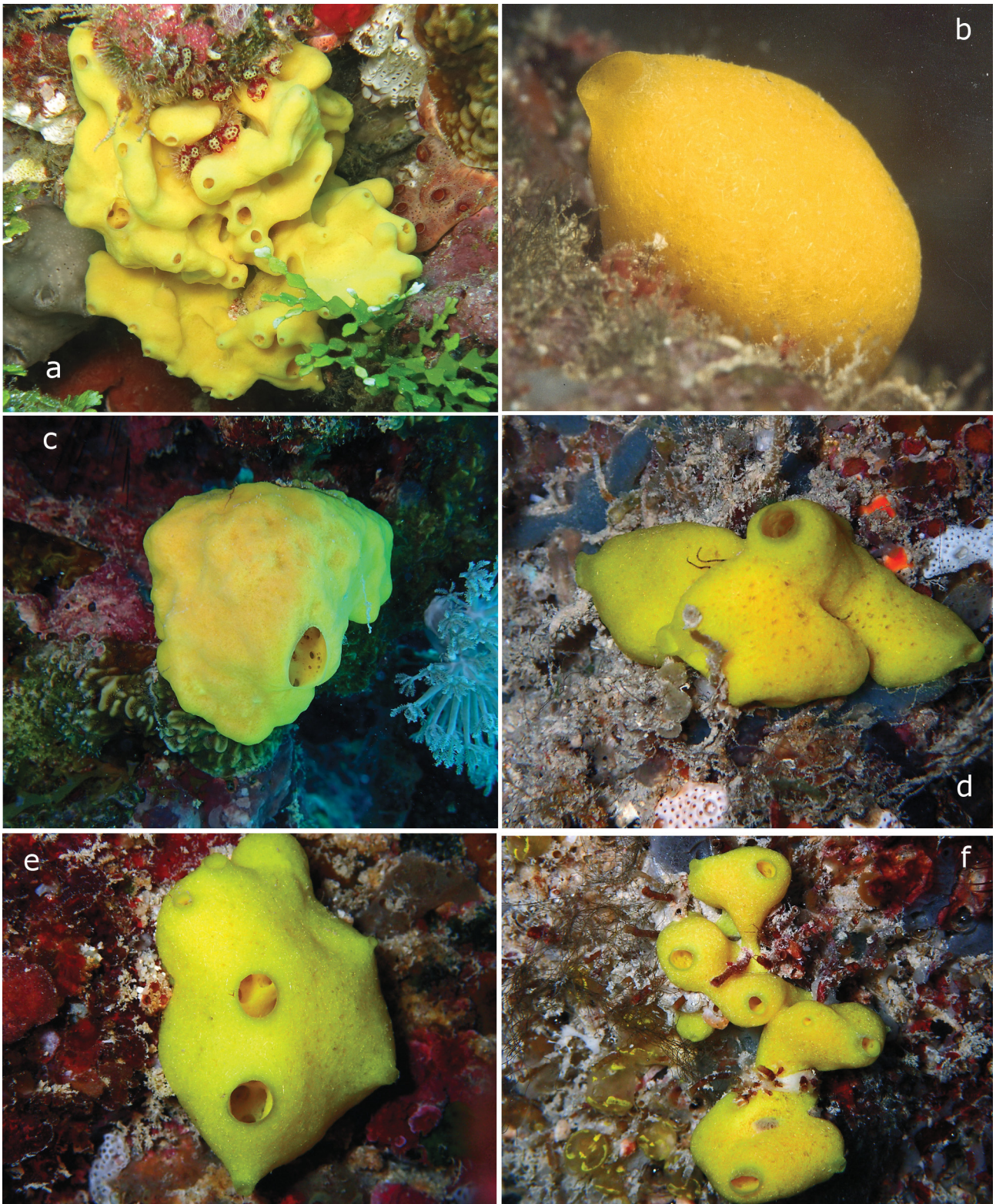


FIGURE 43. *Leucetta chagosensis* Dendy, 1913, habitus in situ of selected specimens, a, RMNH Por. 10114 from the Maldives, b, ZMA Por. 13480, from Aqaba, Red Sea, c, RMNH Por. 9638 from Jeddah, Red Sea, d, RMNH Por. 11657 from Rodrigues, e, RMNH Por. 11601 from Rodrigues, f, RMNH Por. 11658, from Rodrigues (all photos N.J. de Voogd, except ZMA 12480, photo M. Wunsch).

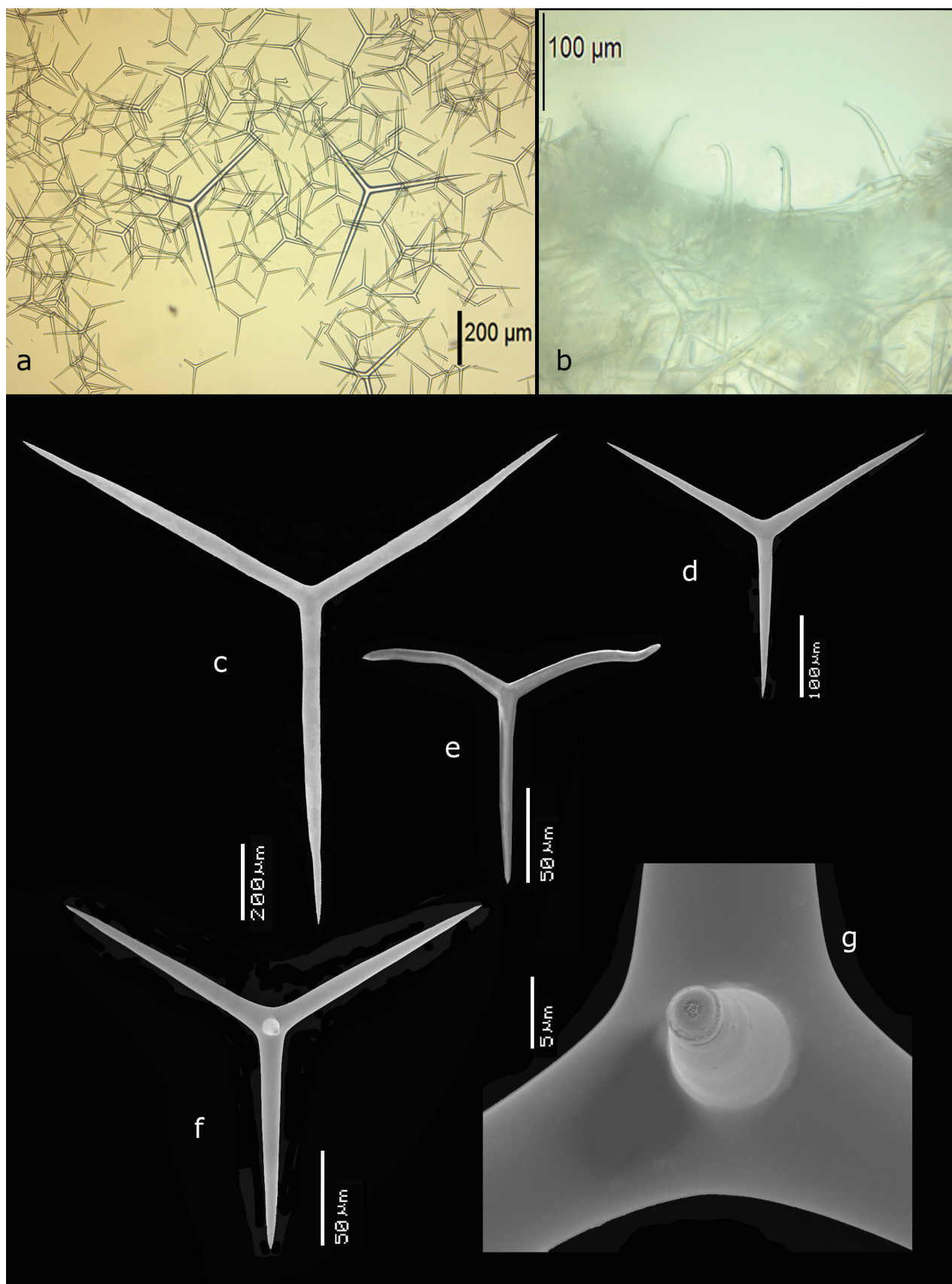


FIGURE 44. *Leucetta chagosensis* Dendy, 1913, ZMA Por. 21468 from the Red Sea, N of Jeddah, a, light microscopic overview of the spicule complement, b, light microscopic cross section of the atrial wall showing protruding apical actines of the tetractines, c–g, SEM images of the spicules, c, giant triactine, d, small triactine, e, triactine from the oscular rim, f, tetractine, g, detail of apical actine of the tetractine.

***Leucetta microraphis* Haeckel, 1872**

Figs 45a–f, 46a–e

Leucetta primigenia var. *microraphis* Haeckel, 1872: 119, pl. 21 figs 10–17.

?*Leucandra primigenia* var. *microraphis*; Row 1909: 186.

Leucetta microraphis; Van Soest & De Voogd 2015: 54, figs 39a–d, 40a–d, with further synonyms.

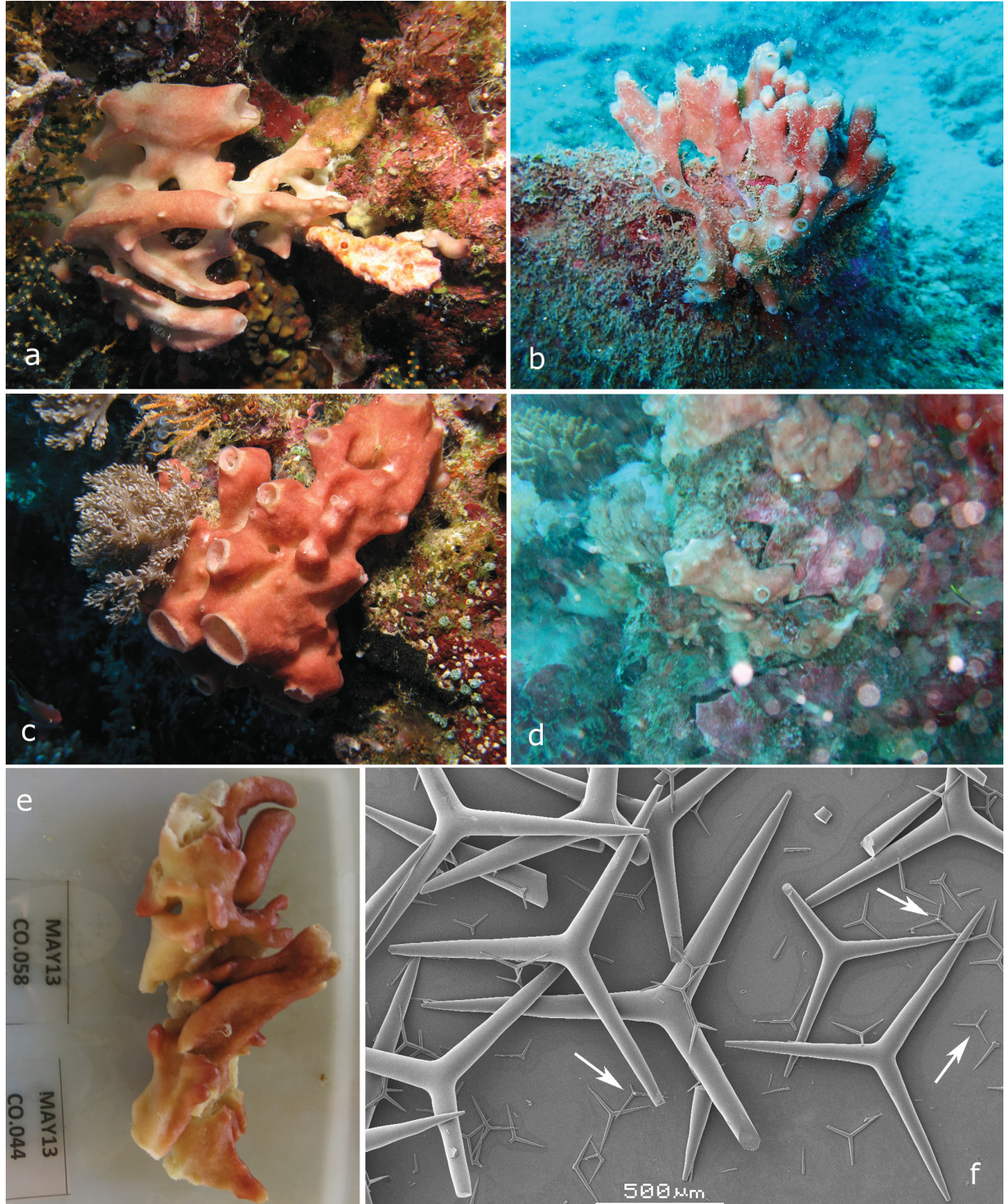


FIGURE 45. *Leucetta microraphis* Haeckel, 1872, from Mayotte and Madagascar, a–d, habitus in situ (photos N.J. de Voogd and A. Bialecki), a, Mayotte RMNH Por. 8341, b, ditto, c, Mayotte RMNH Por. 8318, d, Madagascar RMNH Por. 8717, e, Mayotte RMNH Por. 8341, on deck, f, Mayotte RMNH Por. 8341, SEM image of overview of the spicules showing giant and small triactines from the main skeleton, and tetractines (arrows) from the atrial wall.

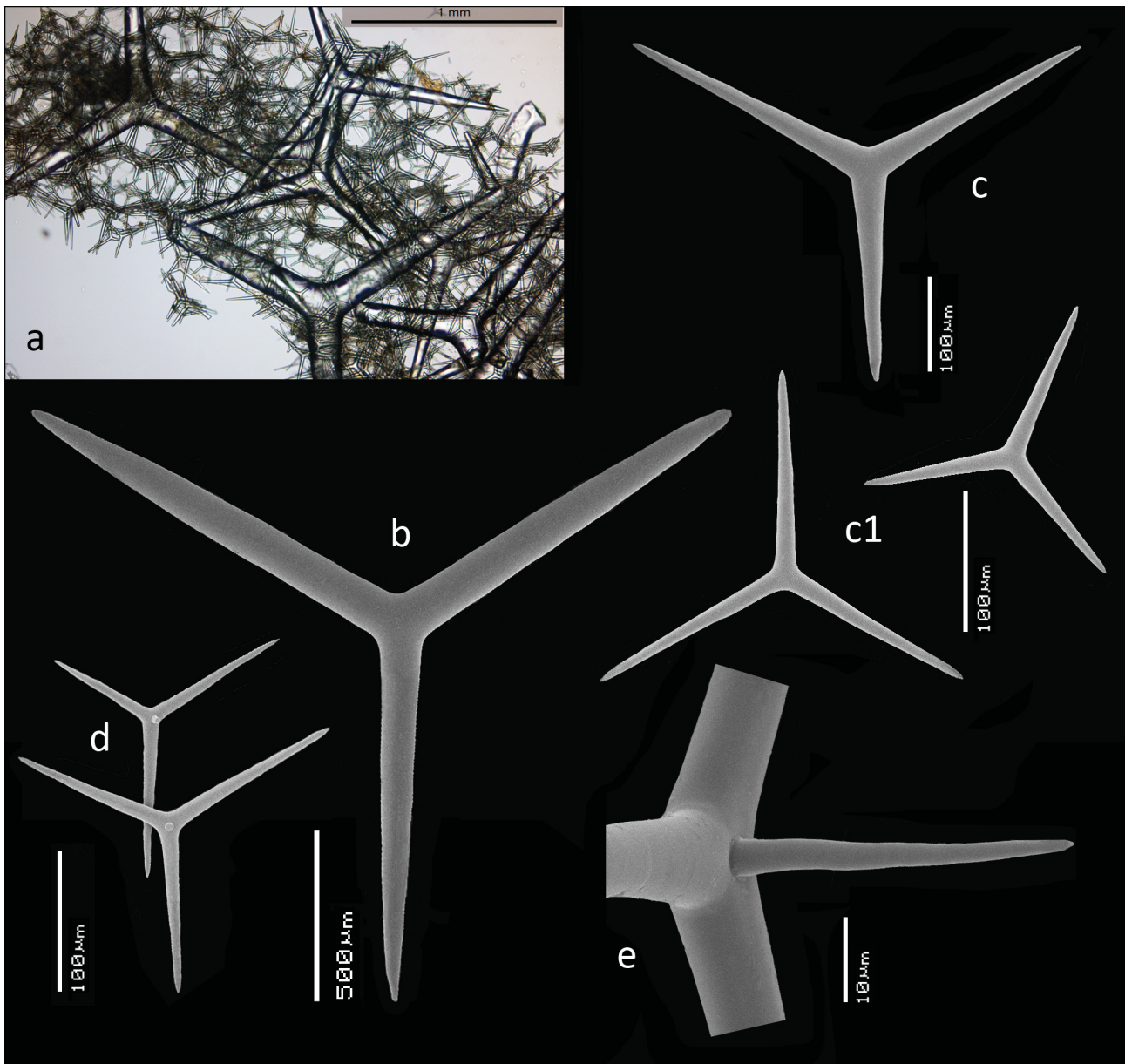


FIGURE 46. *Leucetta microraphis* Haeckel, 1872, RMNH Por. 8318 from Mayotte, a, light microscopic overview of surface skeleton, b–e, SEM images of the spicules, b, giant triactine, c, small triactines, largest sizes, c1, small triactines, smallest sizes, d, tetractines, e, detail of apical actine of tetractine.

Material examined. RMNH Por. 8318, Mayotte, Ankazoberavina, Roland Point, 12.9731°S 44.9793°E, coll. A. Bialecki, field nr. MAY01-018, 4 May 2013; RMNH Por. 8341, Mayotte, Passe Boueni Sud, 12.9265°S 44.9668°E, coll. A. Bialecki field nr. MAY03-41, 5 May 2013; RMNH Por 8717, Madagascar, Riva Be, 12.9849°S 48.3910°E, depth 2–3 m, coll. A. Bialecki, field nr. MAD12-IM047, 27 December 2012.

Description. Because this species was extensively treated recently by Van Soest & De Voogd (2015), we provide here only a summary treatment. The in situ habitus (Figs 45a–d) with its pinkish red-green-brown masses of tubular outgrowths with lighter colored undersides and tube rims, is quite characteristic, leaving no doubt that it is conspecific with Indonesian specimens previously described by us. Tubular outgrowths are 3–6 cm high and 1–2 cm in diameter. Surface optically smooth, but rough. Consistency is firm. On deck habitus (Fig. 45e) similar in color to in situ habitus.

Aquiferous system. Leuconoid

Skeleton. (Figs 45f, 46a) A dense mass of triactines of various sizes, with tetractines lining the atrial cavities. Giant triactines concentrated at the surface.

Spicules. (Figs 46b–d) These include a large size range of giant triactines, small triactines, and tetractines.

Giant triactines (Fig. 46b), equiradiate, equiangular, actines measuring 480–846–1260 x 65–107–155 µm

Small triactines (Figs 46c,c1), equiradiate, equiangular, possibly in two overlapping sizes, actines measuring overall 124–171–216 x 10–15.1–22 µm.

Tetractines (Figs 46d), basal triadial system with actines 78–119–148 x 8–10.3–12 µm, apical actines wobbly (Fig. 46e) or curved, relatively small and thin 14–36–48 x 4–5.7–7 µm.

Distribution and ecology. Mayotte, Madagascar, Red Sea, Indonesia, Australia, Papua New Guinea, New Caledonia, on reefs in shallow depths.

Remarks. This species is reported throughout the Indo-West Pacific tropical region, but the identities of all these records need critical re-examination. The present specimens conform closely in habitus and color to the Indonesian specimens described by us previously (Van Soest & De Voogd 2015), but the giant triactines are smaller and thinner in the present specimens. The habitus does not seem to match in some aspects with e.g. Wörheide & Hooper's (1999) Australian record and with Voigt *et al.*'s (2017) Red Sea records, as these specimens lack the red-brown-greenish pink-with-white coloration characteristic of our concept of this species. Spicule sizes of the triactines of these latter records do match better with those of the present specimens. Critical comparison with uniformly pinkish white specimens is made below.

We obtained partial 28S rRNA sequences from several Western Indian Ocean specimens (Mayotte and Madagascar), downloaded several more from Indonesia and Australia. Oliver Voigt's Red Sea sequences were made available to us. All are presented in Fig. 2C. They are discussed below in the Remarks of a new species, *L. sulcata* **sp.nov.** from Rodrigues.

Row's (1909) records of two specimens from the northern and southern parts of the Red Sea were not described, so these remain *incertae sedis*.

Thacker *et al.* (2013) reported the West Indian species *Leucetta primigenia* Haeckel, 1872 from Malaysia. This likely concerns *Leucetta microraphis*.

***Leucetta pyriformis* Dendy, 1913**

Figs 47a–c, 48a–e

Leucetta pyriformis Dendy, 1913: 11, pl. 1 fig. 7, pl. 4 fig. 3.

? *Leucetta microraphis*; Voigt *et al.* 2017: 21, figs 12a–d (cf. below).

Material examined. RMNH Por. 9528, Saudi Arabia, Jeddah, near Thuwal, Shi'b Nazer (exposed), 22.303417°N 39.048917°E, depth 6 m, scuba, coll. N.J. de Voogd. field nr. THU02/JED011, 6 November 2014; ?ZMA Por. 10461, Seychelles, Mahé, NE coast, North East Point, 4.5833°S 55.4667°E, depth 0–5 m, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 604, 8 December 1992.

Description. In situ these are globular to lobate, white-transparent sponges (Figs 47a–b), with at the surface giant triactines clearly visible to the naked eye. There is a narrow atrial cavity in the center of the lobes, ending in an oscule with small rim. Largest individual lobe 3 cm high, 2 cm in diameter. Preserved fragments (Fig. 47c) are yellowish white in color and rough looking and feeling. Consistency firm to hard.

Aquiferous system. Leuconoid.

Skeleton. Dense mass of triactines, with giant triactines especially numerous at the surface, and with tetractines at the atrial surface.

Spicules. Giant triactines, small triactines, and tetractines. The Saudi Arabian material is slightly different from the Seychelles material and both differ slightly from Dendy's type specimens from Cargados Carajos, so we provide spicule data for all specimens separately.

RMNH Por. 9528: Giant triactines (Fig. 48a), equiradiate, equiangular, 504–1073–1711 x 61–131.8–204 µm; ZMA Por. 10461: 354–852–1470 x 42–109.8–181 µm; Dendy (1913): 1000 x 100 µm.

RMNH Por. 9528: Small triactines (Figs 48b), equiradiate, equiangular, 102–191–234 x 11–14.9–24 µm, some smaller sagittal triactines (Fig. 48c) with wavy paired actines may represent spicules from the oscular rim; ZMA Por. 10461: 132–182–222 x 11–14.8–19 µm; Dendy (1913): 170 x 12.5 µm, including some sagittal triactines.

RMNH Por. 9528: Tetractines, (Fig. 48d) basal radiate system similar to triactines, but actines smaller and thinner, 121–152–184 x 8–11.7–14 µm; apical actines (Fig. 48e) relatively long, straight, sharply pointed,

47–99–146 x 3–8.1–11 μm ; ZMA Por. 10461, respectively 133–161–201 x 9–12.9–17 μm and 41–118–164 x 5–9.2–11 μm ; Dendy (1913): similar in size to triactines, apical actine long and slender.

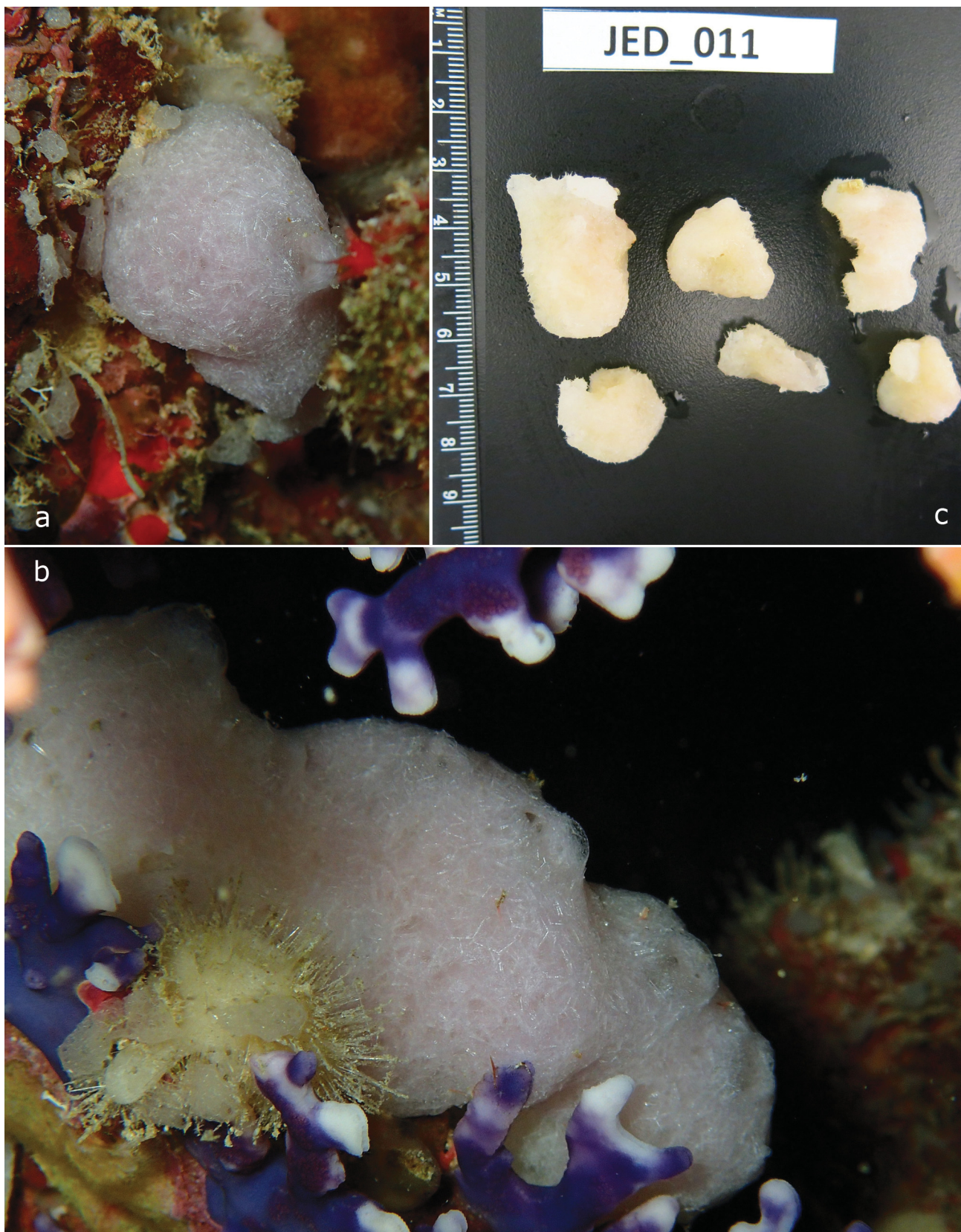


FIGURE 47. *Leucetta pyrifomis* Dendy, 1913, RMNH Por. 9528 from Saudi Arabia, Jeddah, a–b, habitus in situ (photos N.J. de Voogd), c, preserved fragments.

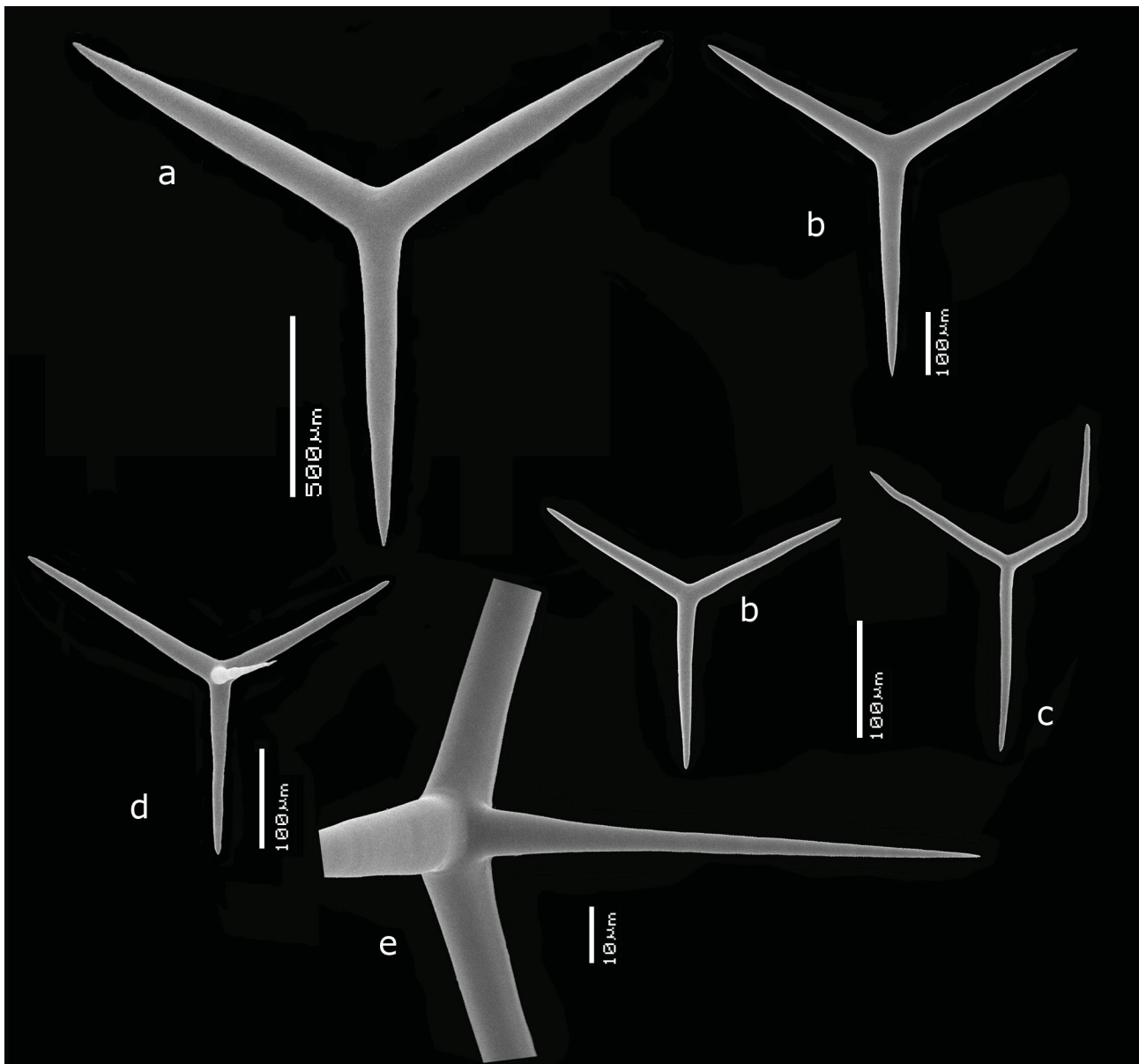


FIGURE 48. *Leucetta pyriformis* Dendy, 1913, RMNH Por. 9528 from Saudi Arabia, Jeddah, SEM images of the spicules, a, giant triactine, b, small triactines, c, cortical sagittal triactine, d, tetractine, e, detail of tetractine showing long thin straight apical actine.

Distribution and ecology. Saudi Arabia, Seychelles, Cargados Carajos, on reefs at shallow depth. Burton (1959) reported this species from the Maldives, but provided no description.

Remarks. Dendy's (1913) type material is similar in shape (although slightly smaller) and also has the giant triactines clearly visible at the surface (cf. Dendy 1913: pl.1 fig. 7). The white live color was not recorded by Dendy. The combination of characters differs clearly from *Leucetta chagosensis* (yellow, smooth, with clearly thinner giant triactines, and the apical actines of the tetractines usually curved) and *L. microraphis* (red-brown-greenish, apical actines of the tetractines thin and usually curved).

Voigt *et al.*'s (2017) record of *L. microraphis* consisted of pinkish white lobes, with prominent oscules. The transparent surface shows giant triactines like in our material, and the apical actines of the tetractines are long, up to $180 \times 13 \mu\text{m}$, so we assume that their record could belong to the present species.

Unfortunately we were not succesfull in obtaining partial 28S sequences.

***Leucetta sulcata* sp.nov.**

Figs 49a–d, 50a–d

Material examined. Holotype, RMNH Por. 11639, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG042, 17 October 2016.

Paratypes, RMNH Por. 11643, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG046, 17 October 2016; RMNH Por. 11645, Mauritius, Rodrigues, Mourouk Ebony, Castel Rock, 19.76203°S 63.46273°E, depth 10 m, scuba, coll. N.J. de Voogd, field nr. ROG048, 17 October 2016.

?Additionally: ZMA Por. 16368, Madagascar, Nosy Bé, Ambariobé, N of Kosy Komba, depth 6–8 m, scuba, coll. J.H. Stock, 28 December 1963.

Description. The in situ shape is a massive lumpy sponge (Fig. 49a) with irregular grooves and deep holes. Live color pale greyish white with pink rims in the peripheral parts. Surface irregular, in places somewhat conulose. Oscules inconspicuous, almost flush with the surface. Color of specimens on deck (Fig. 49b–c) and preserved (Fig. 49d) remains the same. Size of preserved specimens up to 13 x 8 x 8 cm, oscules 5 mm in diameter. Grooves and ridges up to 1 cm wide. Consistency coarse, harsh and hard.

Aquiferous system. Leuconoid.

Skeleton. A dense mass of giant triactines and small triactines. The oscules lead into round atrial cavities lined with tetractines and triactines.

Spicules. (Figs 50a–d) Giant triactines, small triactines, tetractines.

Giant triactines (Figs 50a) equiradiate, equiangular, 408–984–1380 x 43–107.2–204 µm.

Small triactines (Figs 50b) equiradiate, equiangular, 124–186–241 x 10–16.8–22 µm; small sagittal triactines with wavy paired actines (not shown), 83–106–133 x 7–10.2–14 µm.

Tetractines (Figs 50c–d) with basal triradiate system similar to triactines, 102–163–204 x 9–12.6–16 µm, apical actines thin, curved (Fig. 50d), 29–58–96 x 3–5.2–8 µm.

Distribution and ecology. Rodrigues, possibly Madagascar, on reefs in shallow depth.

Etymology. Sulcatus (L.) meaning grooved, referring to the habitus.

Remarks. The spicule sizes and shapes are similar to those of *Leucetta microraphis*, to which the present species is most closely related. Two small irregular fragments of a white sponge, ZMA Por. 16368, collected near Nosy Bé, Madagascar, could belong to the present species based on its skeleton and spicules, but the small material without a definite shape precludes a definite conclusion.

We obtained sequences of the holotype and two of the paratypes and in our phylogenetic analysis (Fig. 2C) they grouped together (at 85% bootstrap value) in a larger clade containing sequences of *L. microraphis* from Mayotte, Madagascar, Australia and the Red Sea. Aligned and trimmed sequences of this larger *L. microraphis*-group (length 396 sites), showing 19 non-conserved sites, resulted in observed differences of 2–8 sites between *L. sulcata* sp.nov. and various sequences of *L. microraphis* s.l. The four sequences of *L. sulcata* sp.nov. shared two unique non-conserved sites. The three sequences of *L. microraphis* with pinkish red-brown-green color, described above from Mayotte and Madagascar, shared three unique non-conserved sites. These were not shared by the one Indonesian sequence of a specimen with similar morphology as the Mayotte and Madagascar specimens.

Remarkably, Oliver Voigt's Red Sea sequences did not have any uniquely shared sites, individual sequences sharing non-conserved sites variously with *L. sulcata* sp.nov. or Western Indian Ocean *L. microraphis*, and the Australian and Indonesian sequences. Clearly, the morphological discrepancies and inconsistencies in *L. microraphis* s.l. are not easily solved by molecular sequence data. *L. microraphis* s.l. are likely a complex of sister species. The morphological differences of the present new species (white color, grooved and holed habitus) with *L. microraphis* s.s. (pinkish red-brown-green tubular masses) preclude conspecificity. The pink-white Red Sea specimens and *L. pyriformis* specimens described above are additional members of the group, differing in shape, color and e.g. in the long straight vs. curved condition of the apical actines of the tetractines. More study is necessary to differentiate the species.

Leocorny *et al.* (2016) recently studied the *Leucetta* species from (sub-)tropical Australian waters: *Leucetta prolifera* (Carter, 1878) (originally as *Teichonella*), *L. insignis* Row & Hozawa, 1931, *L. infrequens* Row & Hôzawa, 1931, *L. expansa* Row & Hôzawa, 1931, *L. villosa* Wörheide & Hooper, 1999, *L. foliata* Leocorny *et al.*, 2016 and *L. purpurea* Leocorny *et al.*, 2016. Of these species, two are slightly similar to the new species in having

a folded habitus, *L. prolifera* and *L. foliata*, but the former has the folds broadly bladed with rows of oscules on the upper surface of the folds, whereas the latter has the folds sharply and thinly bladed. Both do not really resemble the irregularly grooved-holed specimens of the new species. Both species have next to the usual complement of giant triactines, small triactines and small tetractines also large tetractines of the same size or larger as the giant triactines. The remaining species have a more compact or globular habitus, also unlike our new species: *L. insignis* is shaped like *L. chagosensis* but has tripod-like giant triactines, *L. infrequens* is a small erect clump, which apparently lacks small tetractines, *L. expansa* is also a small, but squat clump, possessing ectosomal microdiactines in addition to the usual spicule complement, *L. villosa* is provided with villous hair-like outgrowths on the surface, and finally *L. purpurea* is a small globular purple-colored sponge with giant tripods, sharing this feature with *L. insignis*.



FIGURE 49. *Leucetta sulcata* sp.nov., habitus in situ, on deck and preserved, a, holotype RMNH Por. 11639 in situ at Rodrigues, b, paratype RMNH Por. 11643, on deck, Rodrigues, c, paratype RMNH Por. 11645, on deck, Rodrigues, (photos N.J. de Voogd), d, paratype RMNH Por. 11643, preserved, Rodrigues.

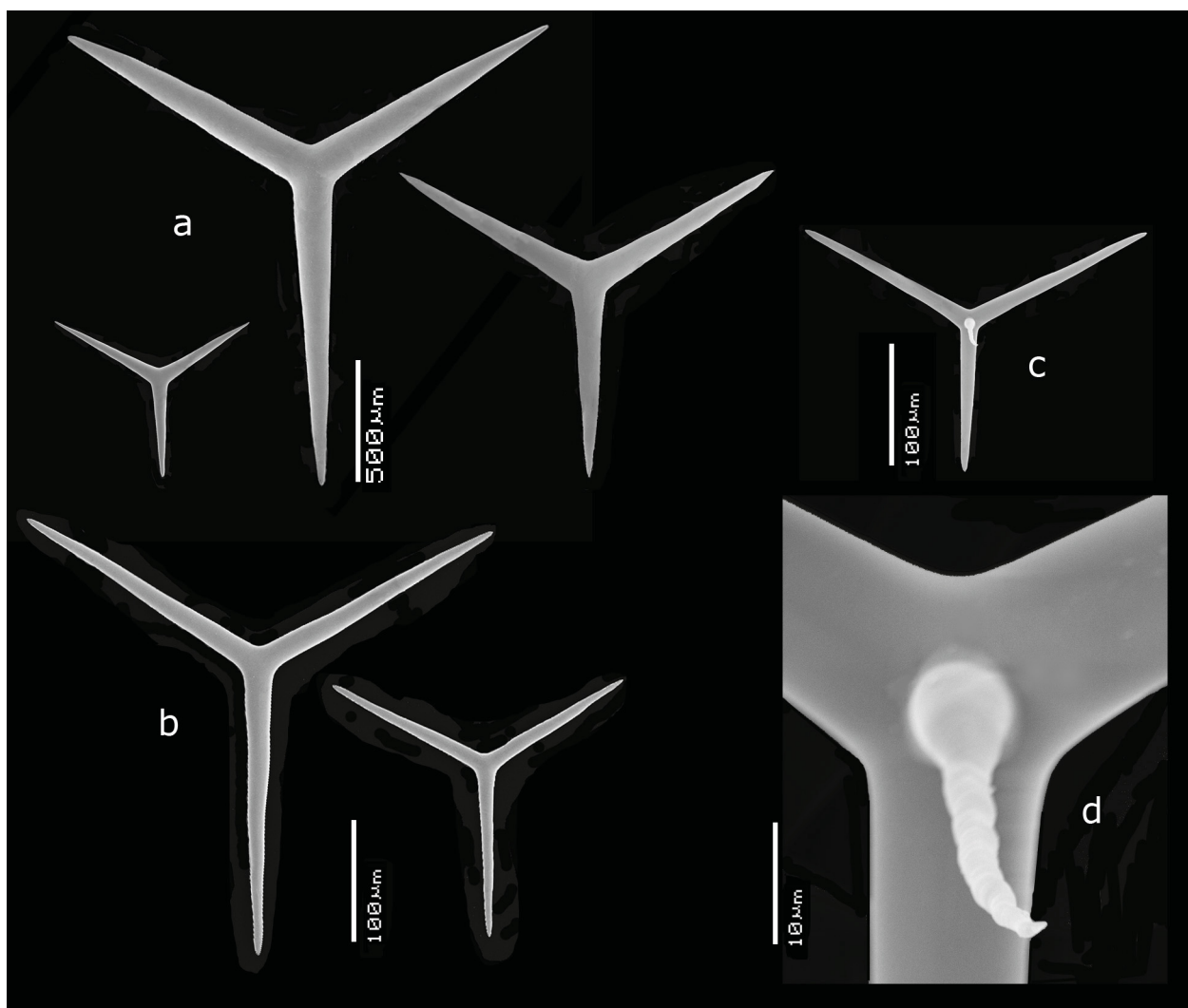


FIGURE 50. *Leucetta sulcata* sp.nov., holotype RMNH Por. 11639 from Rodrigues, SEM images of the spicules, a, giant triactines, b, small triactines, c, tetractine, d, detail of tetractine showing thin curved apical actine.

Genus *Pericharax* Poléjaeff, 1883

Pericharax orientalis Van Soest & De Voogd, 2015

Figs 51a–h

Pericharax heteroraphis; sensu Dendy 1913: 13 (not: *Pericharax carteri* var. *heteroraphis* Poléjaeff, 1883: 66).

Pericharax orientalis Van Soest & De Voogd, 2015: 57, figs 41a–e, 42a–e.

Material examined. RMNH Por. 10157, Maldives, Faafu Atoll, Wallstreet, 3.119°N 72.979556°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. MAD10/MAS118, 20 February 2015; ZMA Por. 17996, Mauritius, 20.0304°S 57.5364°E, depth 7–28 m, scuba, coll. P. Daniel Marie, field nr. MO4SP5TB, 2014; ZMA Por. 18308, Mauritius, 20.0378°S 57.5361°E, depth 10–20 m, scuba, coll. P. Daniel Marie, field nr. 5, December 2014; ZMA Por. 21792, Mauritius, depth 10–20 m, scuba, coll. P. Daniel Marie, field nr. VI sp.17, December 2010.

Description. Since this species was treated extensively recently (see Van Soest & De Voogd, 2015), we provide here only a short description. Large, yellow-green, upright or volcano-shaped sponges (Fig. 51a), with faintly ridged or shallowly grooved sides and prominent wide central vent or oscule. Occasionally two or more individuals are attached forming a small group. Sizes up to 10 cm or more in height, 10 cm or more in diameter. Surface may be covered in tiny tubes of syllid worms. In preservation, specimens become red-brown (Fig. 51b). Consistency hard, rough to the touch.

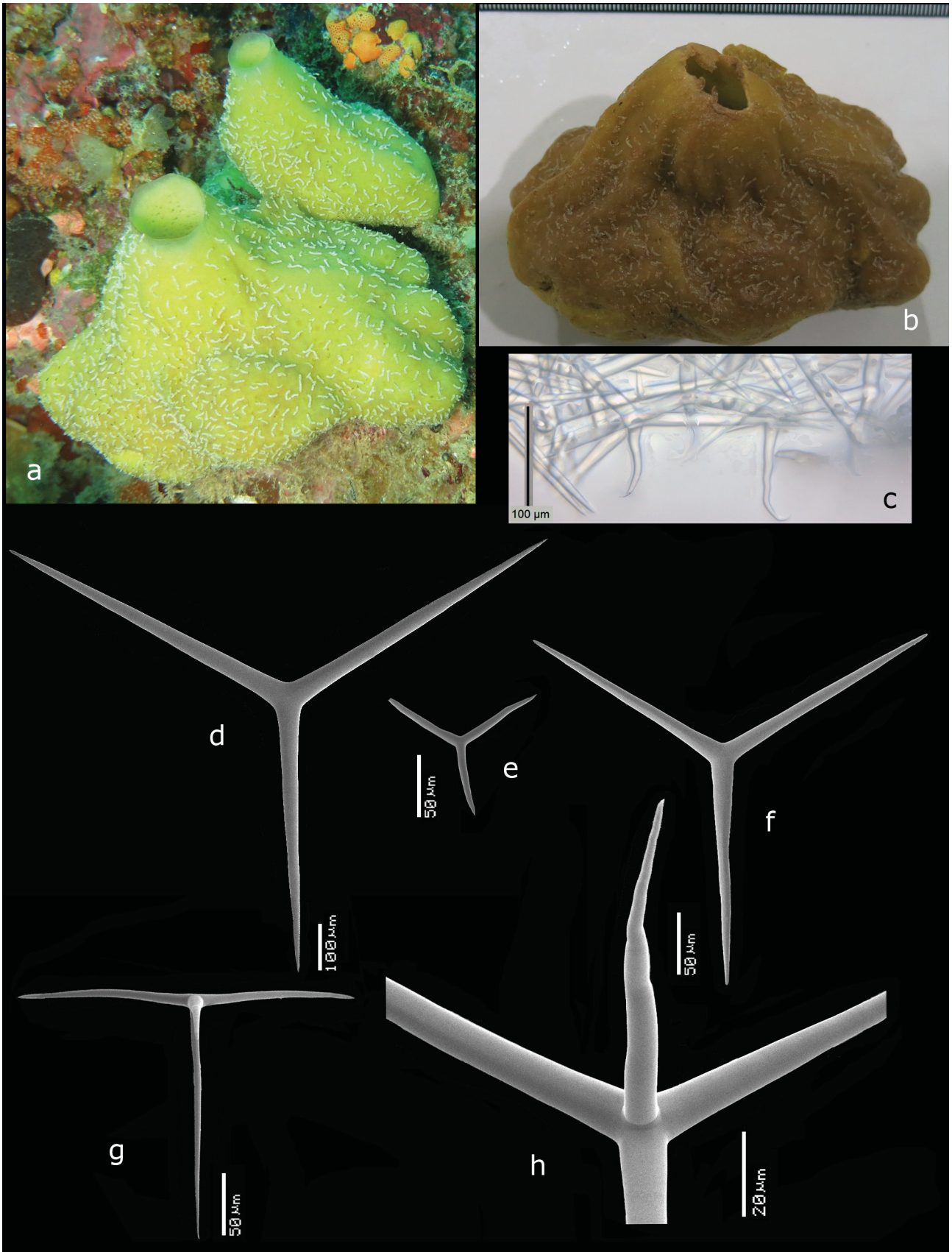


FIGURE 51. *Pericharax orientalis* Van Soest & De Voogd, 2015, RMNH Por. 10157, from the Maldives, a, habitus in situ (photo N.J. de Voogd), b, on deck, c, cross section of atrial wall to show apical actines of the tetractines protruding in the atrial lumen, d–h, SEM images of the spicules, d, giant triactine, e, cortical triactine, f, small triactine, g, tetractine, h, detail of g showing thin apical actine.

Aquiferous system. Leuconoid.

Skeleton. Cortical region with a thin layer of small sagittal triactines forming rounded subdermal spaces, carried by tangentially arranged subcortical giant triactines. Choanosomal skeleton built predominantly by small triactines supporting the leuconoid canal system. The atrial walls are formed predominantly by tetractines with their apical actines protruding into the atrial cavity (Fig. 51c).

Spicules. (Figs 51d–h) Giant triactines, small cortical triactines, small choanosomal triactines, atrial tetractines.

Giant triactines (Fig. 51d), equiradial, equiangular, $396\text{--}1386\text{--}2310 \times 28\text{--}124.3\text{--}222 \mu\text{m}$.

Cortical triactines (Fig. 51e), irregular, slightly sagittal, with all three actines slightly different and somewhat wavy, $54\text{--}88\text{--}119 \times 6\text{--}8.1\text{--}11 \mu\text{m}$.

Small triactines (Fig. 51f), regular, equiradial, equiangular, $126\text{--}181\text{--}228 \times 12\text{--}15.9\text{--}23 \mu\text{m}$.

Tetractines (Figs 51g–h), with basal radiate system equiradial, equiangular, actines $106\text{--}156\text{--}192 \times 7\text{--}11.3\text{--}17 \mu\text{m}$, apical actines (Fig. 51h) thin, mostly wavy or curved, but may be straight, $25\text{--}67\text{--}108 \times 4\text{--}6.4\text{--}10 \mu\text{m}$.

Distribution and ecology. Maldives, Mauritius, elsewhere widely distributed in the Indo-West Pacific tropical region, on reefs down to 20 m or deeper.

Remarks. *Pericharax peziza* Dendy, 1913 is a small cup-shaped sponge, pale yellow in alcohol, which has not been found again after its original description from Cargados Carajos. Its skeletal architecture and spiculation is similar to *P. orientalis*.

We obtained sequences of the holotype of *Pericharax orientalis* from Indonesia (RMNH Por. 5259) and of the above described RMNH Por 10157 from the Maldives and in our phylogenetic analysis (Fig. 2C) both ended up in the same clade at moderate bootstrap value.

Recently, Leocorny *et al.* (2017) described several new *Pericharax* species from Western Australia, *P. vallii* Leocorny *et al.*, 2017, and *P. crypta* Leocorny *et al.*, 2017. These species clearly differ from the present specimens in aspects of habitus and spicule sizes. Leocorny *et al.* (2017) found that *Leucetta* and *Pericharax* could not be retrieved as monophyletic, and this is confirmed in our Fig. 2C.

Subclass Calcaronea Bidder, 1898

Order Leucosolenida Hartman, 1958

Family Grantiidae Dendy, 1893

Genus *Grantia* Fleming, 1828

Grantia aff. *indica* Dendy, 1913

Figs. 52a–e, 53a–f

? *Grantia indica* Dendy, 1913: 20, pl. 2 fig. 3, pl. 4 figs 4–5.

Material examined. ZMA Por. 10223b, Seychelles, Mahé, NE coast, Cap Maçons and Anse de Forbans, 4.7667°S 55.5167°E , depth 0–6 m, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 612, 12 December 1992; ZMA Por. 11566b, Seychelles, Amirantes, Île Desnoeufs platform, outer slope, 6.2167°S 53.0167°E , depth 12–15 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 738/22, 2 January 1993; ZMA Por. 11749, Seychelles, Amirantes, Île Desnoeufs platform, outer slope, 6.2167°S 53.0167°E , depth 12–15 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 738/24, 2 January 1993.

Description. Small white, very ‘hairy’, sycon-like individuals (Fig. 52a). Largest specimen squat, 5 mm high, 4 mm in diameter, but smaller specimens (Figs. 52b–c) may be more elongate. Fringe of long diactines (Figs 52b, d) about 1 mm long.

Aquiferous system. Syconoid.

Skeleton. (Figs 52d–e) Skeleton articulate, with long diactines protruding obliquely from the surface, cortical skeleton a layer of larger and smaller sagittal triactines, tubar skeleton consists of rows of triactines. Subatrial skeleton of sagittal tetractines, atrial skeleton of tetractines with long apical actines, protruding into the atrial lumen

(Fig. 52e). Fringe consists of long diactines supported by sagittal tetractines (Fig. 52d).

Spicules. (Figs. 53a–f) Diactines, trichoxeas, sagittal triactines, and sagittal tetractines.

Diactines of the main body (Fig. 53a), inequilateral, blunt at the proximal end, sharp at the distal end, quite variable in length both in the same specimen and among specimens, $276\text{--}641\text{--}1022 \times 10\text{--}19.4\text{--}24 \mu\text{m}$.

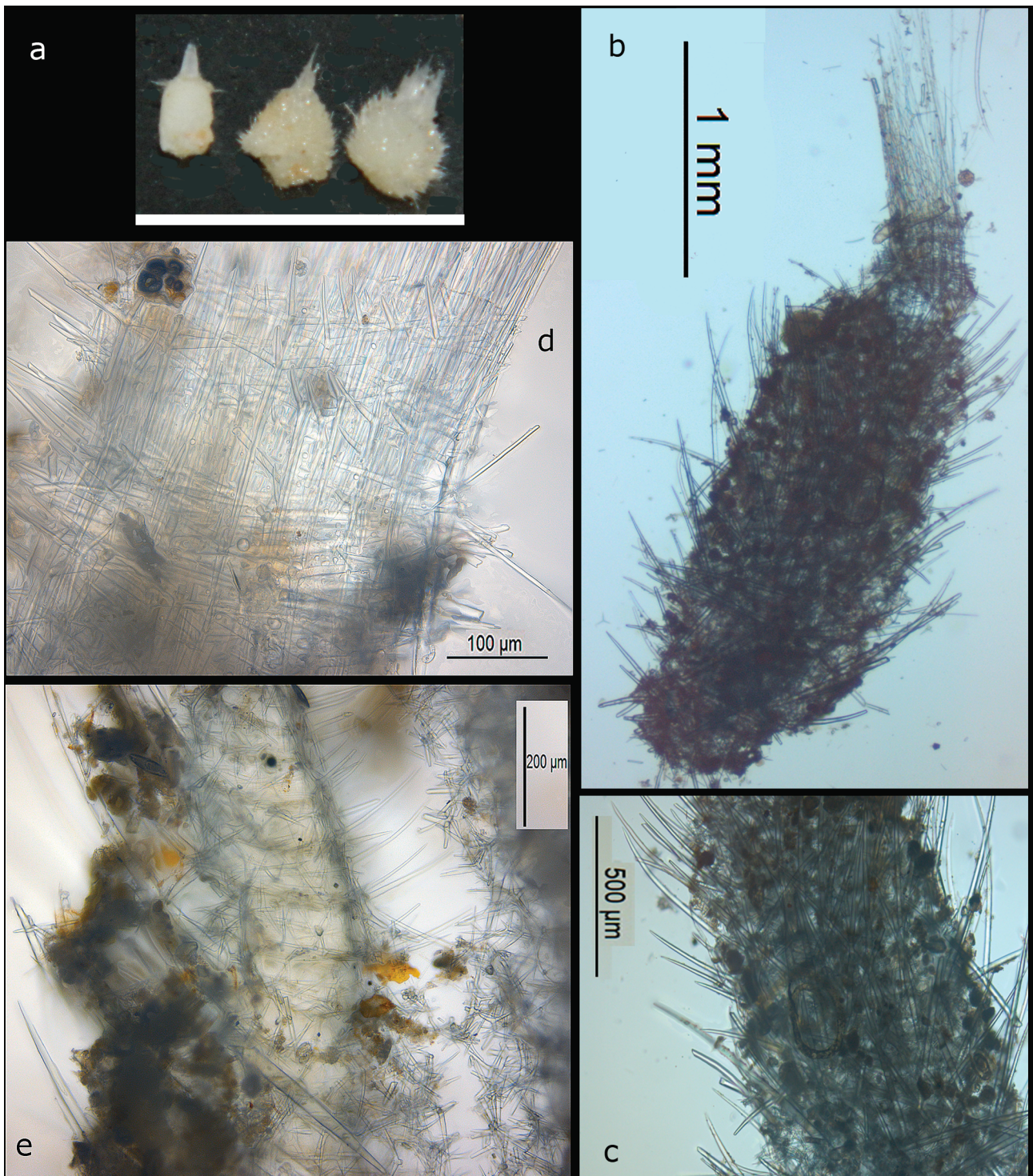


FIGURE 52. *Grantia* aff. *indica* Dendy, 1913, ZMA Por. 11556b, from the Seychelles, a, three individuals (scale bar = 1 cm), b, light microscopic image of small individual, c, detail of the same, d, light microscopic image of the fringe of trichoxeas supported by tetractines, e, cross section of body wall and atrium, showing syconoid structure and apical actines of atrial tetractines protruding in the atrial lumen.

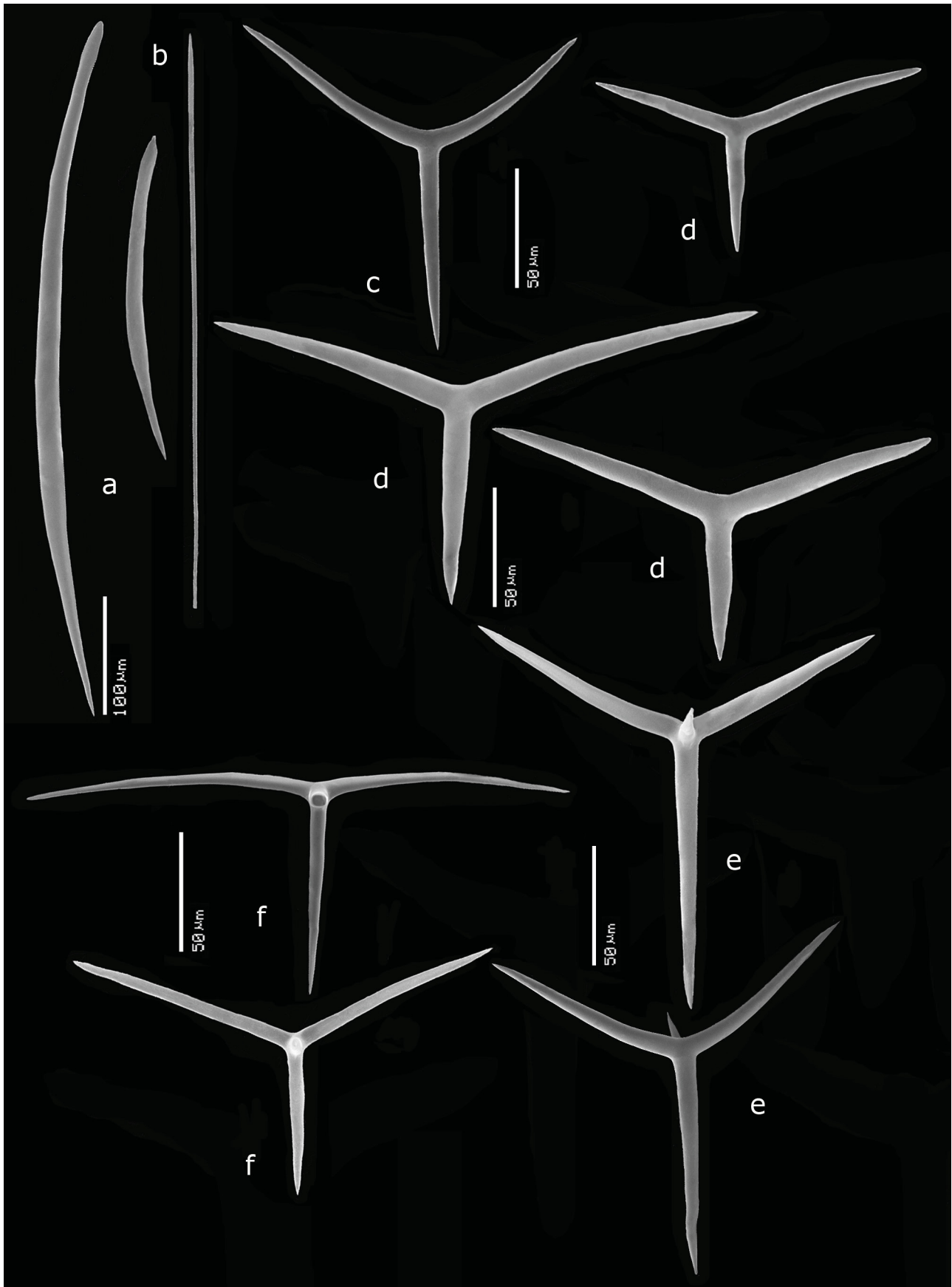


FIGURE 53. *Grantia* aff. *indica* Dendy, 1913, ZMA Por. 11556b, SEM images of the spicules, a, diactines of the cortical skeleton, b, broken fragment of trichoxea from the fringe, c, cortical triactine, d, tubar triactines, e, subatrial tetractines, f, atrial tetractines.

Trichoxeas (Fig. 53b) of the fringe, inequidended with one end slight swollen and the other sharply pointed, often broken, length of the larger fragments 420–970–2000 μm , thickness 1.5–4.1–8 μm .

Cortical triactines (Fig. 53c), sagittal with oxborn-shaped paired actines; unpaired actines 33–108–165 \times 4–6.7–12 μm , paired actines 66–80–99 \times 4–5.9–7 μm .

Tubar triactines (Figs 53d), sagittal, with straight or slightly curved paired actines, occasionally T-shaped; length of unpaired actines 45–73–120 \times 6–9.4–13 μm , paired actines 66–102–156 \times 7–9.7–12 μm ; these also occur in a low number in the fringe.

Subatrial and fringe tetractines (Figs 53e), unpaired actine usually longer than paired actine, with short apical actine; unpaired actines 78–114–156 \times 7–8.4–11 μm , paired actines 48–90.0–104 \times 7–7.7–9 μm , apical actines 14–23–39 \times 3–4.7–7 μm . They occur also in the fringe.

Atrial tetractines (Figs 53f), with straight unpaired actines, almost straight paired actines and long slightly curved apical actines; unpaired actines 105–139–174 \times 8–8.3–10 μm , paired actines 90–132–171 \times 6–7.2–8 μm , apical actines 54–128–210 \times 5–7.8–9 μm .

Distribution and ecology. Seychelles, shallow reef down to 15 m.

Remarks. The present material shares the shape and the composition of the spicule package with Dendy's (1913) type, but almost all spicules are smaller and thinner. Dendy is known to frequently cite only the largest measurements for a spicule category. The type was larger (10 \times 4.8 mm) than our specimens and that may be an additional cause of the spicule size differences, but it is also possible that our material belongs to a closely related separate species, hence our 'aff.' designation. For the time being we emphasize the shared characters.

Unfortunately, our attempt to obtain 28S rRNA sequences failed.

Sycon tabulatum (Schuffner, 1877) (originally as *Sycandra*) has similar shape, but the radial tubes are crowned by a conus of small diactines and there are no giant diactines. The original combination is preoccupied by *Sycandra tabulata* Hackel, 1872. Below (section 'Additional species..'), a new name for Schuffner's species is proposed.

Genus *Ute* Schmidt, 1862

Ute insulagemmae sp.nov.

Figs 54a–e, 55a–g

Material examined. Holotype, ZMA Por. 11562, Seychelles, Amirantes, St. François Atoll, Île Bijoutier, reef, 7.0833°S 52.7333°E, depth 6–18 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 792/03, 5 January 1993.

Description. Twin urn-shaped individuals (Fig. 54a) joint at the base, with a narrow oscule each provided with a short naked collar. Color in life pale orange, in preservation shiny white. Length 1.3 cm, diameter of an individual 5 mm. Surface smooth. Consistency firm.

Aquiferous system. Syconoid.

Skeleton. (Figs 54b–e) A thin cortical skeleton of very small triactines (Figs 54b,d) forming small meshes of 50–70 μm diameter covers a subcortical layer of lengthwise arranged giant diactines (Figs 54b–d). This in turn overlies an articulated skeleton (Figs. 54c,e) of larger triactines. Subatrial skeleton of tetractines and triactines, overlying the atrial skeleton (Fig. 54e) of tetractines with their apical actines protruding in the atrial lumen.

Spicules. (Figs 55a–g) Giant diactines, cortical small triactines, tubar triactines, (sub)atrial triactines, (sub)atrial tetractines, trichoxeas.

Giant diactines (Fig. 55a), fusiform, slightly curved or straight, equidended, 256–1509–2520 \times 13–68.1–116 μm .

Cortical triactines (Figs 55b), sagittal, with strongly irregular paired actines and conical unpaired actines, occasionally reduced to conical tyle, unpaired actines 5–9.4–18 \times 2–4.1–6 μm , paired actines 21–35–51 \times 2.5–3.6–4 μm .

Tubar triactines (Figs 55c), sagittal, but unpaired and paired actines usually not much different in lengths, paired actines straight or slightly curved, (overlapping in shape and size with subatrial triactines); possibly divisible in subcortical (larger) triactines and genuine (smaller) tubar triactines, but this was not readily visible; unpaired actines 52–79.5–112 \times 8–10.2–13 μm , paired actines 69–85.1–117 \times 7–8.8–13 μm .

Subatrial triactines (Fig. 55d), strongly sagittal with unpaired actines distinctly longer than paired actines; unpaired actines 91–168–203 \times 9–12.4–15 μm , paired actines 78–97–112 \times 9–12.2–14 μm .

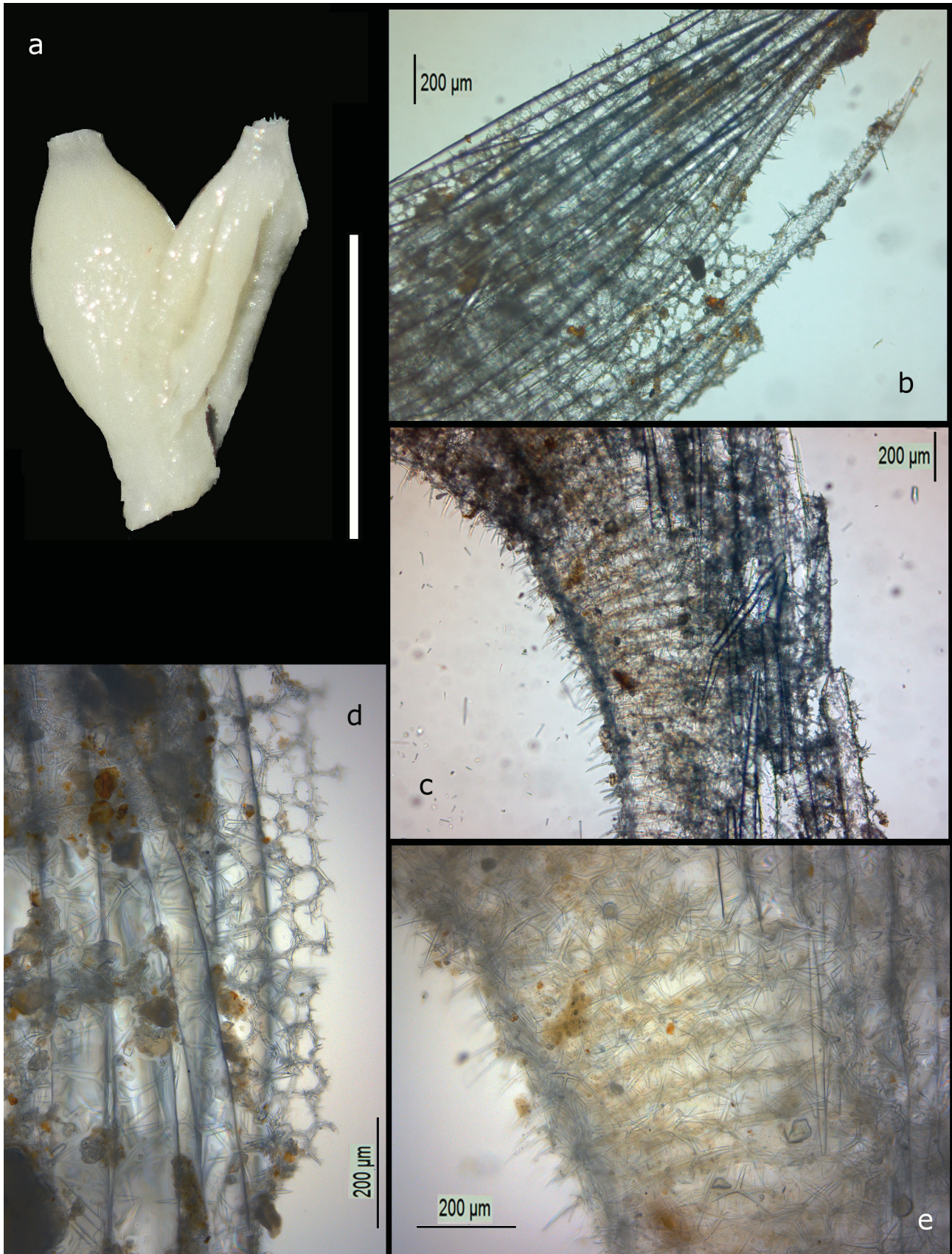


FIGURE 54. *Ute insulagemmae* sp.nov., holotype ZMA Por. 11562, from Île Bijoutier, Seychelles, a, preserved habitus (scale bar = 1 cm), light microscopic image of surface skeleton, c, ditto of cross section of body wall, d, enlarged view of b, showing meshes made up of cortical triactines overlying subcortical giant diactines, e, enlarged view of c showing syconoid skeleton and protruding apical actines of atrial tetractines.

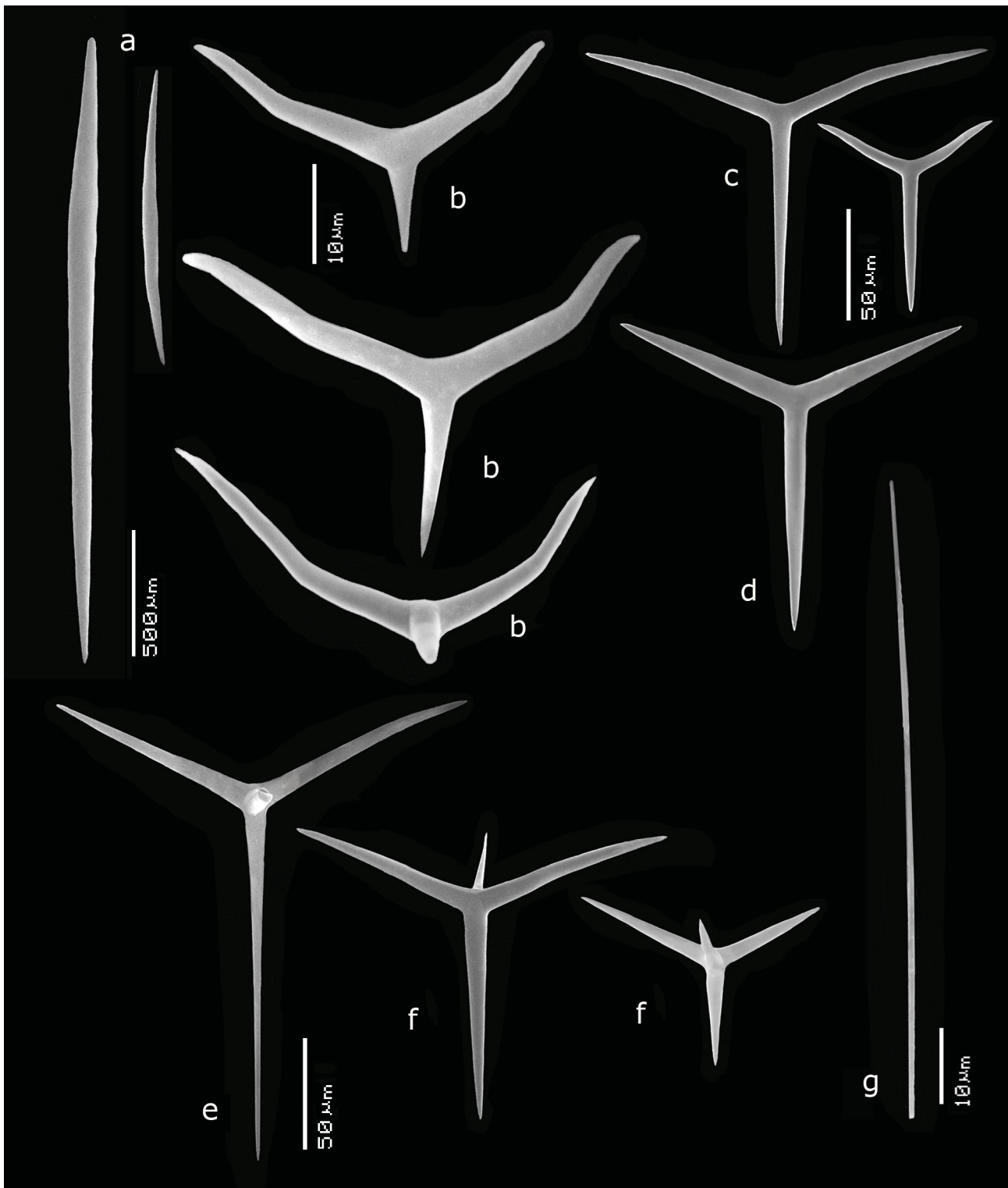


FIGURE 55. *Ute insulagemmae* **sp.nov.**, holotype ZMA Por. 11562, SEM images of the spicules, a, diactines, b, cortical triactines, c, tubar triactines, d, subatrial triactines, e, subatrial tetractine, f, atrial tetractines, g, broken trichoxea from the short oscular collar.

Subatrial tetractines (Fig. 55e), recognizable by a long thinly tapering unpaired actine, which may occasionally have a distal swelling; unpaired actines 171–202–241 x 8–10.2–11 µm, paired actines 76–109–126 x 10–11.3–12 µm, apical actines curved 49–60.4–71 x 6–7.1–8 µm.

Atrial tetractines (Figs 55f), sagittal, with prominent curved apical actines; unpaired actines 61–107.6–165 x 7–8.6–11 µm, paired actines 68–104–126 x 6–8.3–10 µm, apical actines 40–115–201 x 6–8.4–11 µm.

Trichoxeas (Fig. 55g), from the short oscular collar, invariably broken, fragments measure 180–650 x 2 µm.

Distribution and ecology. Known only from the type locality on the outer reef of Île Bijoutier, at 6–18 m depth.

Etymology. The name is a noun composed of insula (L.) = island, gemma (L.) = jewelry, referring to the type locality Île Bijoutier ('jewelry island').

Remarks. Wörheide & Hooper (2003) described *Ute ampullacea* from the Great Barrier Reef, NE Australia. This has similar habitus and spiculation, but the cortical skeleton consists of microdiactines, whereas in the new species these are replaced by irregular small triactines (Fig. 55b). We obtained molecular data for the new species and compared these with GenBank sequences of *Ute* and *Synute*. Remarkably, in our Calcaronea phylogeny (Fig. 3) *Ute ampullacea* and our new species do not show close relationship, as the former ended up in a group of Lelapiidae. The nearest species to *Ute insulagemmae* **sp. nov.** appear to be Australian *Ute* aff. *syconoides* (Carter, 1886) and Australian *Synute pulchella* (Dendy, 1892), which grouped in a well-supported clade (86% bootstrap value) with our new species. Separate inspection of a trimmed alignment of 404 sites of these three species, showed 19 non-conserved sites indicating that the species are probably not closely related. No other *Ute* species have been reported from the tropical Indo-West Pacific.

The *Ute* group appeared in our Calcaronea phylogeny (Fig. 3) in the midst of a group of Heteropiidae and Jenkinidae. We interpret this result as evidence of insufficient taxon support for our Calcaronea phylogeny.

Genus *Leucandra* Haeckel, 1872

Leucandra pulvinar (Haeckel, 1872)

Figs 56a–d, 57a–e

Sycolepis pulvinar Haeckel, 1870: 251 (*nomen nudum*)

Mlea dohrnii Miklucho-Maclay MS in Haeckel, 1872: 162 (*nomen nudum*)

Leucortis pulvinar var. *semitica* Haeckel, 1872: 163

Leucandra pulvinar; Dendy 1905: 234 (listed, not described)

Material examined. ZMA Por. 13423, Israel, Stylus Pinnacle, Gulf of Aqaba, depth 9 m, scuba, coll. M. Wunsch, field nr. AQ77, 6 July 1998; ZMA Por. 13615, Israel, NW of harbor, Gulf of Aqaba, under overhang on harbor pile, depth 12 m, scuba, coll. M. Wunsch, field nr. AQ39, 3 July 1998.

Description. Whitish or pale yellow globular-lobate sponges (Figs 56a,d) with optically smooth or irregular hispid surface, approximately 3 x 2 x 1.5 cm. Both specimens have two prominent oscules, 3–4 mm in diameter, with naked collar, leading to atrial spaces that are shallow and narrow. In preserved condition the color is beige-dirty white (Fig. 56b). Consistency brittle, firm.

Aquiferous system. Leuconoid.

Skeleton (Fig. 56c). A thin cortical skeleton of sagittal triactines covering tangential giant diactines arranged in all directions. There are also tangential trichoxeas. Choanosomal skeleton a confused mass of irregular triactines with scattered diactines of all sizes. Atrial skeleton consists of small irregular triactines.

Spicules (Figs 57a–e). Diactines, trichoxeas, sagittal triactines, irregular triactines. No tetractines.

Diactines fusiform (Figs 57a,a1), varying in size from giant to very small, 105–929–2760 x 11–47–108 µm.

Trichoxeas (Figs 57b,b1), often broken, but also varying in length, 123–465–1200 x 1.5–3.4–7 µm.

Cortical triactines (Fig. 57c), predominantly sagittal, almost T-shaped, with unpaired actine shorter than paired actines, although equiactinal spicules also occur, unpaired actines 90–143–212 x 9–14.7–20 µm, paired actines 165–198–270 x 14–16.3–21 µm.

Choanosomal triactines (Fig. 57d), basically equiactinal, but irregularly sagittal or oxhorns-shaped, 168–229–298 x 15–19.1–24 µm.

Atrial triactines (Fig. 62e), smaller than the other triactines, equiactinal, irregularly parasagittal, 45–91–120 x 5–8.1–10 µm.

Distribution and ecology. Red Sea, Sri Lanka, shallow reef localities.

Remarks. Our specimens resemble Haeckel's 1872 description (vol. 2: 163) and figures (vol. 3: pl. 29 figs 1–10) of *Leucortis pulvinar* var. *semitica*. Next to this variety, Haeckel also described a var. *indica*. Since he did not

describe a typical, separate variety one of the two varieties (*semitica* or *indica*) has to be the nominotypical variety (ICZN art. 47) *Leucortis pulvinar* var. *pulvinar*. In the absence of previous treatments of this problem, we choose here the var. *semitica* as the nominotypical variety to take the name *pulvinar*, as it is the first mentioned. It is likely that both varieties belong to the same species, but a formal synonymization must await the description of recent Indian material. Dendy's (1905) Sri Lanka record of *Leucandra* (*Leucortis*) *pulvinar* remains undescribed.

There are several *Leucandra* species described in the region with similar spiculation, including giant diactines: *Leucandra echinata* Schuffner, 1877 (also reported by Dendy 1913), *Leucandra fascigera* Schuffner, 1877, *Leucandra donnani* var. *tenuiradiata* Dendy, 1916, *Leucandra dwarkaensis* Dendy, 1916 and *Leucandra seychellensis* Hozawa, 1940), but all these have atrial tetractines and differ in habitus. This also applies to two *Leucandra* species from NE Australia, *L. sphaeracella* Wörheide & Hooper, 2003, and *L. nicolae* Wörheide & Hooper, 2003.

Unfortunately, our attempt to obtain a partial 28S sequence failed.

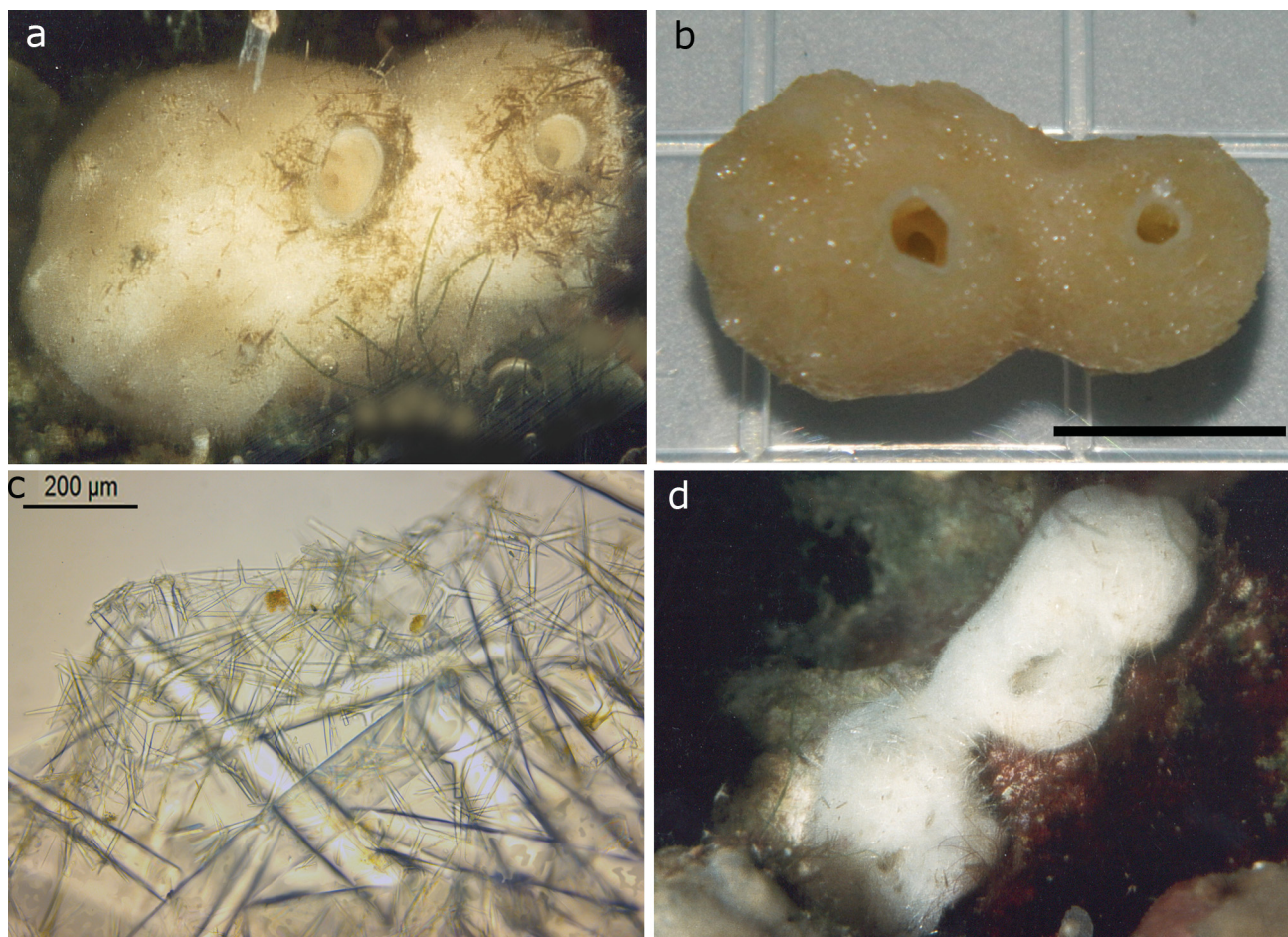


FIGURE 56. *Leucandra pulvinar* (Haeckel, 1872), from Gulf of Aqaba, Red Sea, a, habitus in situ of ZMA Por. 13423 (photo M. Wunsch), b, preserved habitus of the same (scale bar = 1 cm), c, view of surface skeleton of the same, d, habitus in situ of ZMA Por. 13615 (photo M. Wunsch).

Leucandra pilula sp.nov.

Figs 58a–g, 59a–e

Material examined. Holotype, ZMA Por. 10528, Seychelles, Bird Island, 3.7167°S 55.2167°E, coastal reef at 13 m depth, scuba, coll. W. Kolvoort, field nr. NIOP-E stat. 717/34, 20 December 1992.

Paratypes, ZMA Por. 10379a, Seychelles, Mahé, E coast, N of Moyenne Island, 4.6167°S 55.5167°E, depth 1–7 m, reef, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 606, 10 December 1992; ZMA Por. 10641 (2 specimens), Seychelles, Amirantes, St. François Atoll, Île Bijoutier, depth 3 m, reef, scuba, coll. R.W.M. van Soest,

field nr. NIOP-E stat. 792/21, 6 January 1993; ZMA Por. 11564, Seychelles, Amirantes, N of Platte Island Atoll, 5.8167°S 55.3667°E, depth 6 m, reef, coll. R.W.M. van Soest, field nr. NIOP-E stat. stat. 796/42, 7 January 1993.

Description. Small white or beige-white globules (Figs 58a–d), with a single apical oscule, flush with the surface, which is optically smooth but feels rough. Size of body up to 1.5 cm high, 1 cm in diameter; oscule 2–3 mm in diameter. In preservation they stay white. Consistency firm.

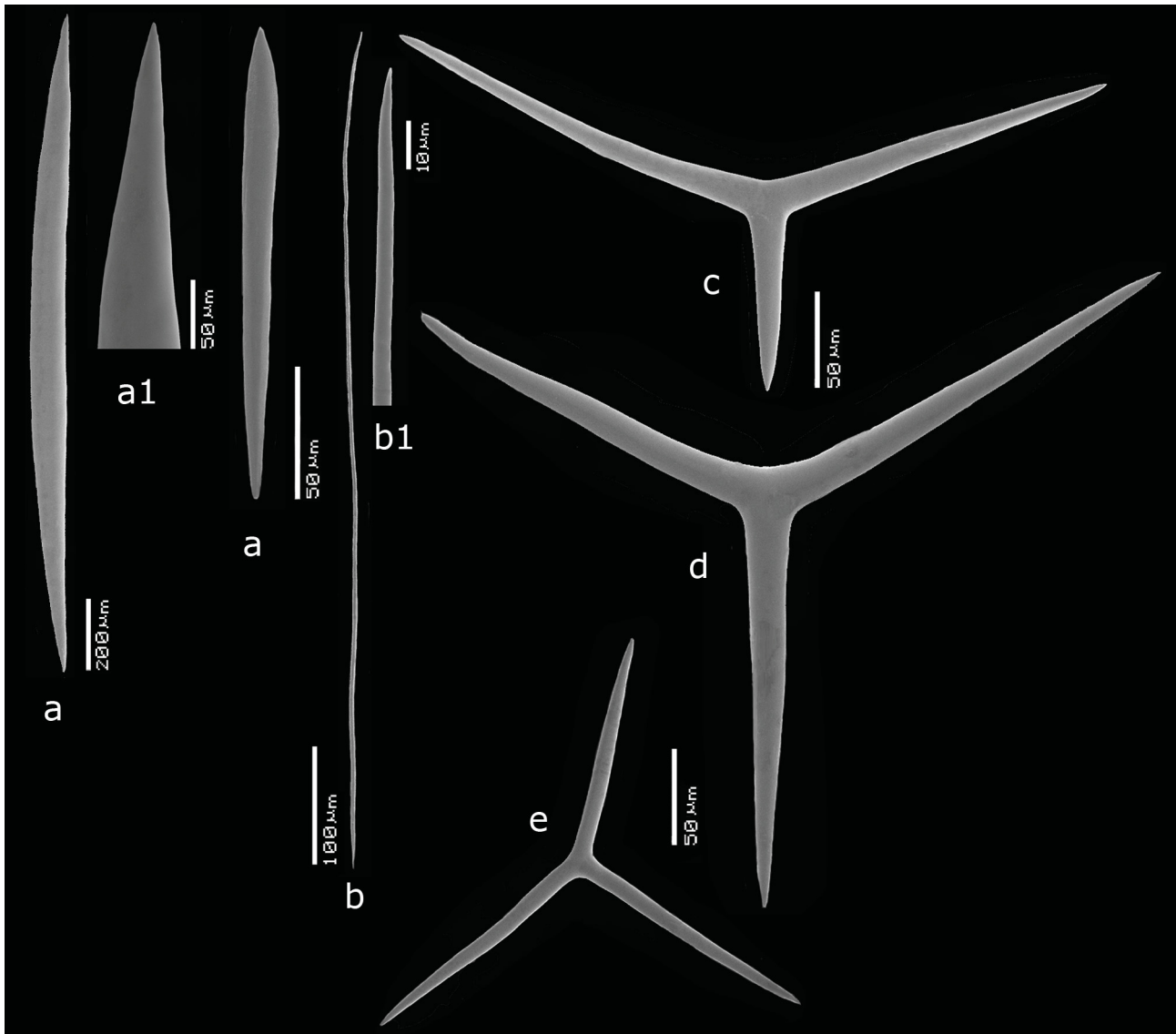


FIGURE 57. *Leucandra pulvinar* (Haeckel, 1872), ZMA Por. 13423, from Gulf of Aqaba, Red Sea, SEM images of spicules, a, giant diactines, a1, detail of sharp end of giant diactine, b, trichoxea, b1, detail of same, c, cortical triactine, d, choanosomal triactine, e, atrial triactine.

Aquiferous system. Leuconoid.

Skeleton. (Figs 58e–g) Cortical skeleton (Fig. 58f) of intermediate sized triactines overlying a mass (Fig. 58e) of giant and smaller triactines forming the choanosomal skeleton supporting the leuconoid aquiferous canal system. The atrial skeleton (Fig. 58g) consists of sagittal triactines and tetractines, the latter with apical actines protruding into the atrial lumen. The oscular rim is supported by trichoxeas.

Spicules. (Figs 59a–e) Giant triactines, oxborn-shaped triactines, small triactines, tetractines, trichoxeas.

Giant triactines (Figs 59a) of the main body wall, actines straight, tapering gradually to sharp points, equiangular and equiradiate or more often sagittal or with all actines of different lengths, 312–628–985 x 19–55.7–93 μm.

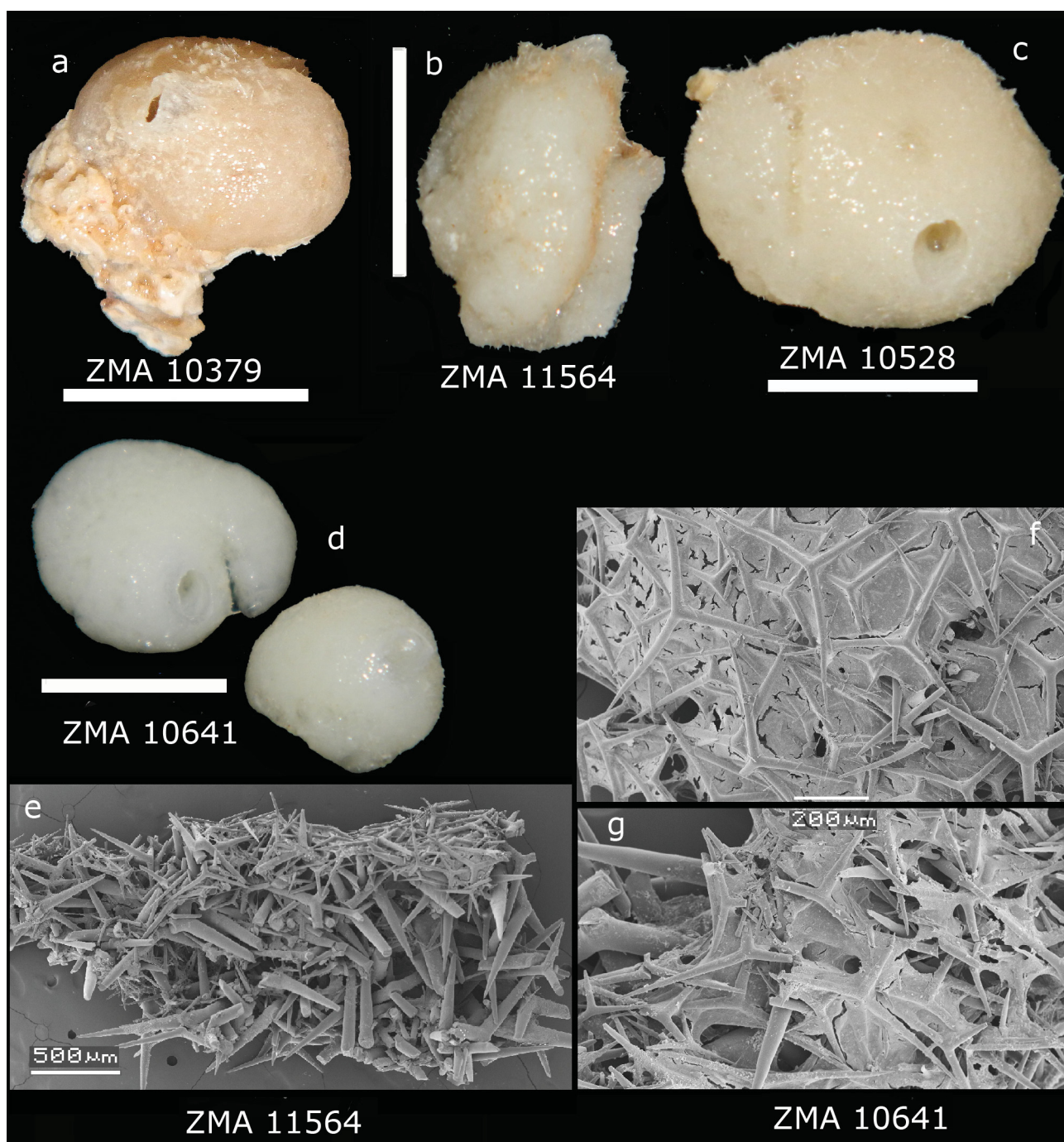


FIGURE 58. *Leucandra pilula* sp.nov., from the Seychelles, a–d, preserved habitus of holotype ZMA Por. 10528 (c) and paratypes ZMA Por. 10379, 11564 and 10641 (a,b and d), e–g, SEM images of the skeleton, e, cross section, f, view of surface skeleton, g, view of atrial skeleton.

Oxhorn triactines (Figs 59b) of the cortical skeleton, sagittal with curved paired actines and straight unpaired actines, unpaired actines 178–245–326 x 15–22.7–31 μm, paired actines 216–281–372 x 16–21.6–28 μm.

Small triactines (Figs 59c) of the main body and the subatrial region, sometimes equiradiate equiangular but more often irregularly sagittal, or T-shaped, unpaired actines 94–172–254 x 9–17.8–26 μm, paired actines 100–186–303 x 11–16.6–29 μm.

Tetractines (Figs 59d) of the atrial skeleton, sagittal, usually with unpaired actine shorter than paired actines, which are usually straight, occasionally slightly curved, unpaired actines 101–186–271 x 14–19.4–32 μm, paired actines 136–239–380 x 9–17.1–32 μm, apical actines slightly curved, 45–84–130 x 4–8.4–11 μm.

Trichoxeas (Fig. 59e) of the oscular region, not common, almost invariably broken, 100–300 x 1–2 μm.

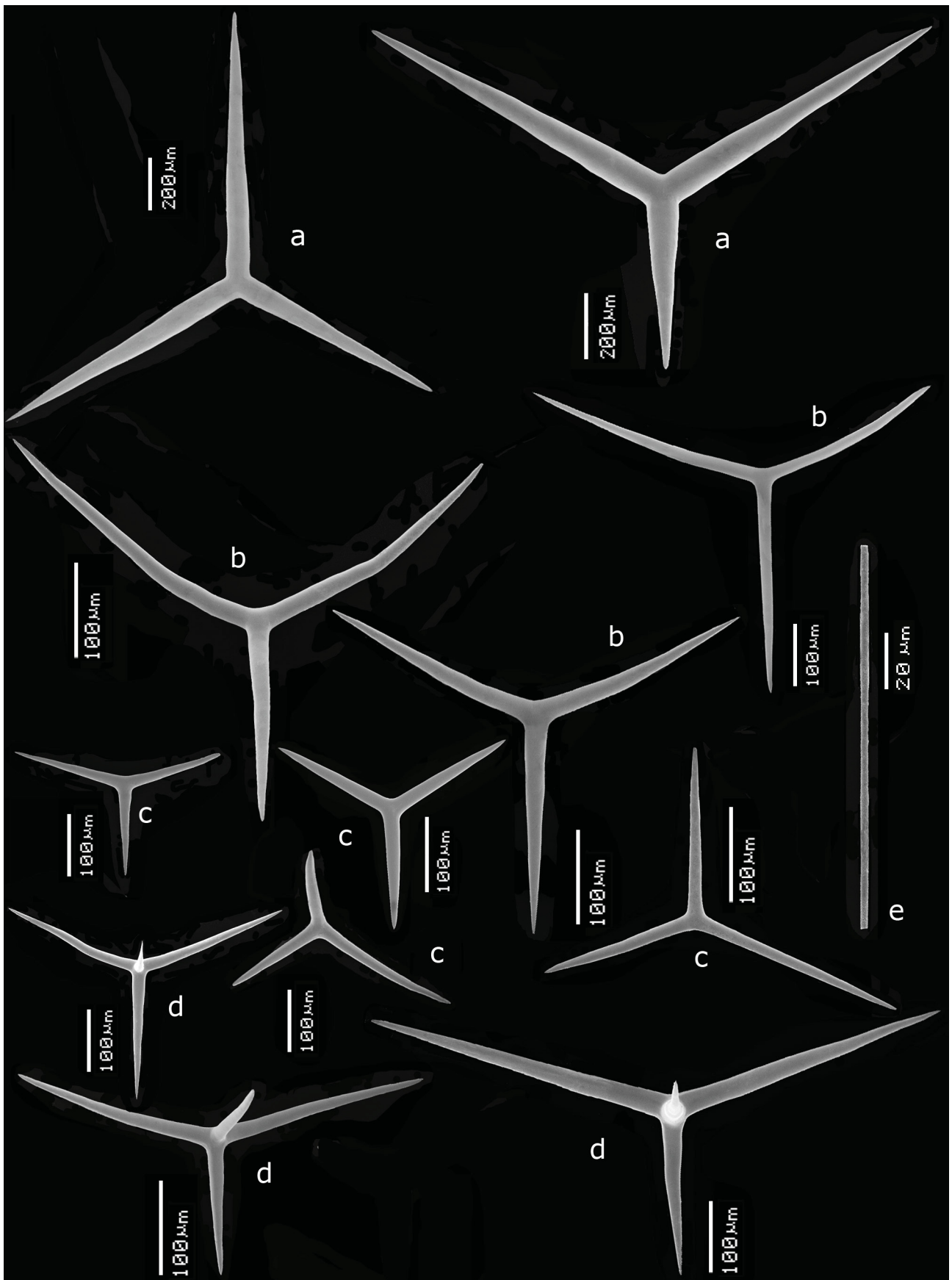


FIGURE 59. *Leucandra pilula* sp.nov., SEM images of the spicules, a, giant triactines of the choanosome, b, cortical triactines, c, small triactines of the choanosome and subatrial region, d, tetractines of the atrial skeleton, e, fragment of trichoxea from the oscular rim.

Distribution and ecology. Seychelles only, but widespread throughout the archipelagoes, on reefs, depths 1–13 m.

Etymology. *Pilula* (L.) = small ball, a noun referring to the habitus.

Remarks. The size of all specimens is uniformly 1–1.5 cm high and 1 cm in diameter, and thus it is likely that this feature is characteristic for the species. The shapes of the triactines and tetractines are somewhat variable among the 5 specimens obtained of this species, but invariably there are giant triactines, smaller cortical triactines and smaller subatrial triactines. The atrial tetractines vary in the length of the paired actines, within and among specimens. However, the overall spicule package is similar in all and the lack of giant diactines is shared by all.

Similar-sized specimens were described by Jenkin (1908) from Zanzibar under the name *Leucandra ananas* (Haeckel, 1872), a species from the Northern Atlantic. This differs clearly by having tufts of large diactines of up to 3000 µm in length projecting from the surface. It is likely an undescribed species.

By the lack of diactines this species stands out among all known *Leucandra* species of the Western Indian Ocean region (but see below). There are no matching descriptions in the region.

We obtained a 28S sequence of the holotype of our new species and compared these to the sequences from GenBank of *Leucandra nicolae* Wörheide & Hooper, 2003 and a new species, *L. mozambiquensis* **sp.nov.** described below. There are no other partial 28SrRNA sequences of *Leucandra* available from the region and moreover the genus has been shown to be non-monophyletic (Dohrmann *et al.* 2006). In our Calcaronea phylogeny (Fig. 3) the three species grouped in a shared clade with modest bootstrap value (52%), with *L. pilula* **sp.nov.** and *L. nicolae* closer (bootstrap value 65 %). A separate inspection of the trimmed alignment of these three species (length 431 sites) showed 15 non-conserved sites, indicating the species are probably not closely related.

***Leucandra mozambiquensis* sp.nov.**

Figs 60a–f, 61a–e

Material examined. Holotype, ZMA Por. 22408a, Mozambique Channel, between Mozambique and Madagascar, E of Juan de Nova Island, 17.2817°S 43.1567°E, depth 60 m, dredged, Pelagia Around Africa Exped.II, leg 6, field nr. 20ASC10, 1 April 2001.

Description. Irregular cup-shaped hollow mass (Fig. 60a) with undulating unequal lumpy walls, size 5 x 5 x 4 cm, walls approximately 1 cm thick. Color in alcohol pale brownish to dirty white. Surface rough. Inner surface of the atrial ‘hollow’ with a few oscular openings of 3–4 mm diameter. Consistency firm but fragile.

Aquiferous system. Leuconoid.

Skeleton. (Figs 60b–f) A cross section (Fig. 60b) shows a confused mass of spicules separated by a clearly developed cortical skeleton (Figs 60c–d) of smaller, mostly sagittal ‘oxhorn’ triactines and a clearly developed atrial skeleton (Figs 60e–f) of atrial tetractines. The choanosomal mass of spicules consists of giant triactines and smaller triactines. Near the atrial skeleton there are also sagittal subatrial tetractines recognizable by unpaired actine of length equal to the paired actines (whereas the atrial tetractines have shorter unpaired actines).

Spicules. (Figs 61a–e) Giant triactines, smaller triactines, atrial and subatrial tetractines.

Giant triactines (Figs 61a) of the choanosomal region, sagittal, usually with unpaired actine shorter than the paired actines, occasionally irregular with actines all of different lengths, actines relatively thin compared to other *Leucandra* species, 471–903–1322 x 30–52.9–72 µm.

Smaller triactines (Figs 61b) of the surface and the choanosome, not clearly differentiated, but either regular or more often ‘oxhorn’-like sagittal with curved and often slightly wobbly paired actines; unpaired actines 184–258–346 x 10–15.6–26, paired actines 191–348–574 x 10–15.9–34 µm.

Tetractines (Figs 61c–d), sagittal, with straight unpaired actines, straight or slightly curved paired actines, and straight or slightly curved apical actines, divisible into subatrially located tetractines with unpaired actines approximately as long as the paired actines, and proper atrial tetractines with unpaired actines clearly shorter than the paired actines.

Subatrial tetractines (Fig. 61c) with unpaired actines measuring 174–221–247 x 8–11.8–15 µm, paired actines 187–239–298 x 11–12.6–15 µm, apical actines 40–55.6–73 x 5–6.7–10 µm.

Atrial tetractines (Figs 61d) with unpaired actines 84–108–151 x 5–8.8–12 µm, paired actines 210–245–289 x 6–9.2–15 µm, apical actines 41–62–92 x 5–6.3–7 µm.

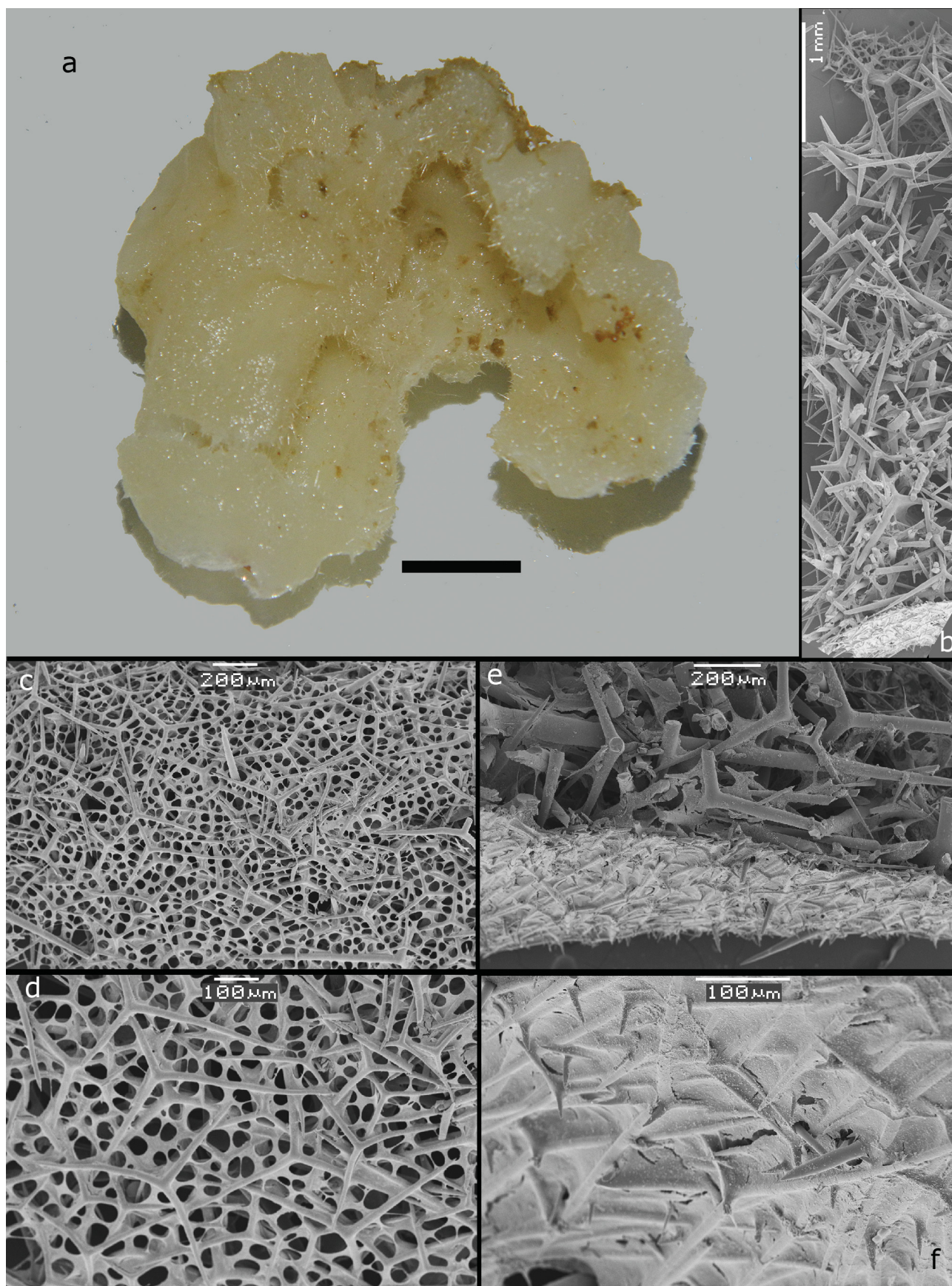


FIGURE 60. *Leucandra mozambiquensis* **sp.nov.**, holotype ZMA Por. 22408a, from northern Mozambique Channel, a, preserved habitus (scale bar = 1 cm), b–f, SEM images of the skeleton, b, cross section (cortical skeleton above, atrial skeleton below), c–d, view of surface and detail, e–f, view of atrial skeleton and detail.

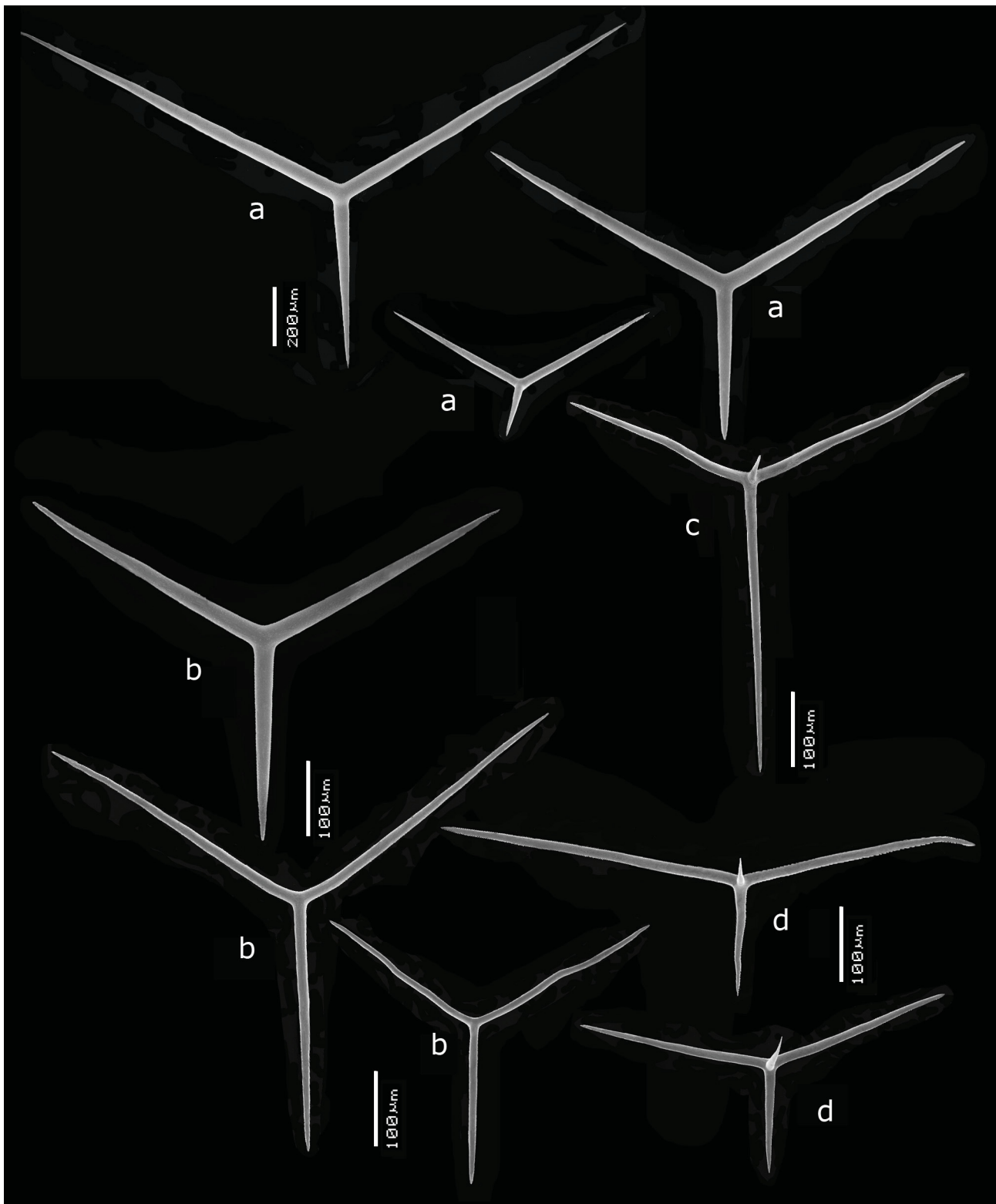


FIGURE 61. *Leucandra mozambiquensis* sp.nov., holotype ZMA Por. 22408a, from northern Mozambique Channel, SEM images of the spicules, a, giant triactines, b, cortical smaller triactines, c, subatrial tetractine, d, atrial tetractines.

Distribution and ecology. Mozambique Channel, on continental platform of NW Madagascar, depth 60 m.

Etymology. Named after the type locality.

Remarks. By the absence of giant diactines, this elaborate species stands out among *Leucandra* species in the region. Only the above described *L. pilula* sp.nov. shares the lack of giant diactines, but that species has radically

different morphology and also the spicules have different dimensions (cf. above). The new species shows morphological similarities to NE Australian *Leucandra nicolae* Wörheide & Hooper, 2003, which also lacks giant diactines and has elaborate shape, but that species has microdiactines lining the choanocyte chambers, which are not present here. The giant triactines of *L. nicolae* have shorter and thicker actines than the present material.

The tetractines of the subatrial region indicate a possible membership of the new species of the genus *Leucandrilla* (cf. below), because subcortical spicules in that genus include tetractines. However, the presence of the long-shafted tetractines in the present material is always close to the atrial skeleton, not in the subcortical region, and they are probably to be considered part of the atrial skeleton.

We obtained a partial 28S sequence of the holotype. In our Calcaronea phylogeny (Fig. 3), the new species grouped together with *L. pilula* **sp.nov.** and *L. nicolae* at a modest bootstrap value (see also above under Remarks of *L. pilula* **sp.nov.**). The relationship with the other two species in the clade is not close.

The nearest group to *Leucandra* in our phylogeny (Fig. 3) is *Paraleucilla*, currently assigned to the family Amphoriscidae. The general lack of sufficient 28S sequences of Calcaronea makes this position debatable. A separate inspection of the trimmed alignment of sequences of the clade of the three *Leucandra* species and the two *Paraleucilla* species (length 423 sites) showed 37 non-conserved sites indicating a large difference between the genera (see also below).

Genus *Leucandrilla* Borojević *et al.* 2000

Leucandrilla aff. *intermedia* (Row, 1909)

Figs 62a–c, 63a–h

?*Leucilla intermedia* Row, 1909: 205, pl. 20 fig.7, textfig. 5.

Leucandra infesta Dendy & Row, 1913: 771.

Material examined. ZMA Por. 13482, Israel, Gulf of Aqaba, Schuhmacher's Pinnacle, depth 2 m, under dead *Acropora*, coll. M. Wunsch, field nr. AQ 126, 10 July 1998.

Description. Spiny-hairy, light green tube (Fig. 62a) attached partially sideways to the substratum. Size 1.5 cm in length and approximately 1 cm in diameter. Terminal oscule naked, 3 mm in diameter. In alcohol (Fig. 62b) the specimen is dirty white. Consistency firm.

Aquiferous system. Syllebeid.

Skeleton. (Fig. 62c) In cross section, the skeleton of the wall shows a cortical layer of small triactines pierced by giant diactines, subcortical skeleton of sagittal large tetractines, choanosomal and subatrial giant, intermediate and small triactines and tetractines, and atrial sagittal triactines and tetractines. The oscular collar contains trichoxeas.

Spicules. (Figs 63a–h) Diactines, triactines, tetractines, trichoxeas,

Giant diactines (Figs 63a,a1) fusiform, tapering to thin points, more or less equiended, 1000–2313–4680 x 24–44.3–50 µm

Cortical triactines (Fig. 63b), slightly sagittal, but equiactinal, 81–114–141 x 7.5–9.3–11 µm

Subcortical large tetractines (Fig. 63c) with apical actines longest and protruding into the choanosome, with unpaired actines 225–276–405 x 18–28.1–44 µm, paired actines 152–238–324 x 15–21.6–30 µm, and apical actines 37–184–390 x 9–21.0–42 µm.

Large triactines (Fig. 63d) and intermediate forms from the choanosomal and subatrial region, slightly sagittal, 165–364–570 x 15–30.9–51 µm.

Large tetractines (Fig. 63e) from the choanosomal and subatrial region, slightly sagittal, unpaired actines 129–227–345 x 15–22.5–34 µm, paired actines 153–249–324 x 12–17.8–24 µm, apical actines 37–53–62 x 8–14.3–19 µm

Atrial triactines (Fig. 63f), sagittal, unpaired actines 63–137–181 x 7–8.8–11 µm, paired actines 141–161–174 x 6–8.6–12 µm.

Atrial tetractines (Fig. 63g), sagittal, with thin sharp apical actines, unpaired actines 96–119–148 x 10–12.0–16 µm, paired actines 123–154–186 x 10–10.8–14 µm, apical actines 15–26.3–37 x 6–8.3–12 µm.

Trichoxeas (Fig. 63h), invariably broken, 800–1000 x 3–3.5 µm.

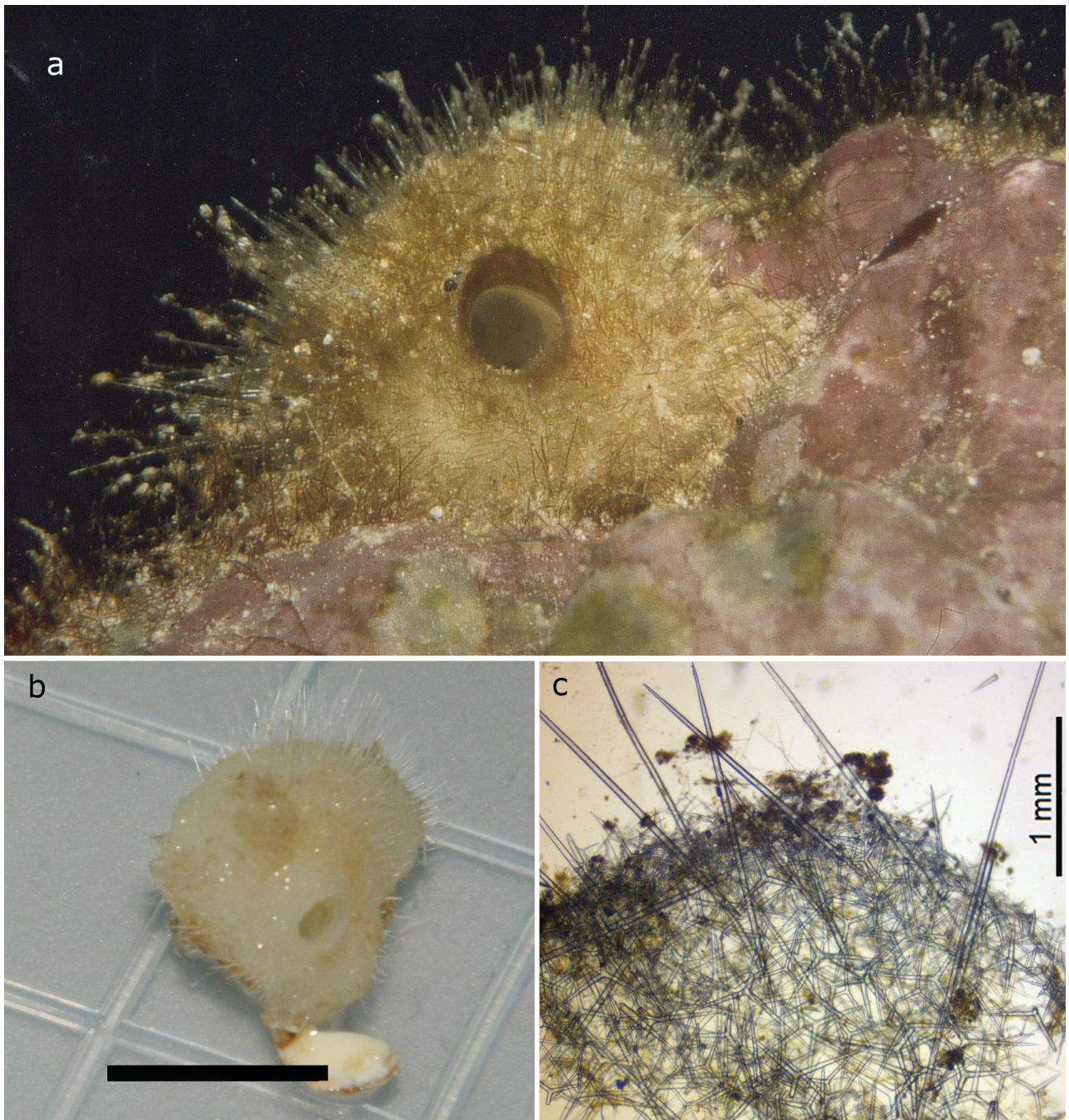


FIGURE 62. *Leucandrilla* aff. *intermedia* (Row, 1909), ZMA Por. 13482, from Gulf of Aqaba, a, habitus in situ (photo M. Wunsch), b, preserved habitus of same (scale bar = 1 cm), c, light microscopic view of peripheral skeleton.

Distribution and ecology. Red Sea, shallow depth.

Remarks. The above-described specimen conforms in most details to Row's description and figures of specimens from Suez. There are slight discrepancies in the spicule sizes, but these are rather generalized in Row's treatment, so this is of not much concern. In contrast to Row's description there are triactines among the atrial spicules in our specimen, which throws some doubt on our identification, hence our assignment to aff. *intermedia*. It cannot be excluded that our material belongs to a different closely similar species.

Dendy & Row's (1913) new name *Leucandra infesta* for the secondary homonymy of Row's *Leucilla intermedia* with Haeckel's (1872) *Leucetta paradoxa* var. *intermedia* has become moot, because the two species involved are now reassigned to different genera. Since the replacement name *L. infesta* was only used once in Burton's (1963) summary of Row's description, which does not count as 'use' in the sense of ICZN art. 59.3, the name *L. intermedia* is reinstated.

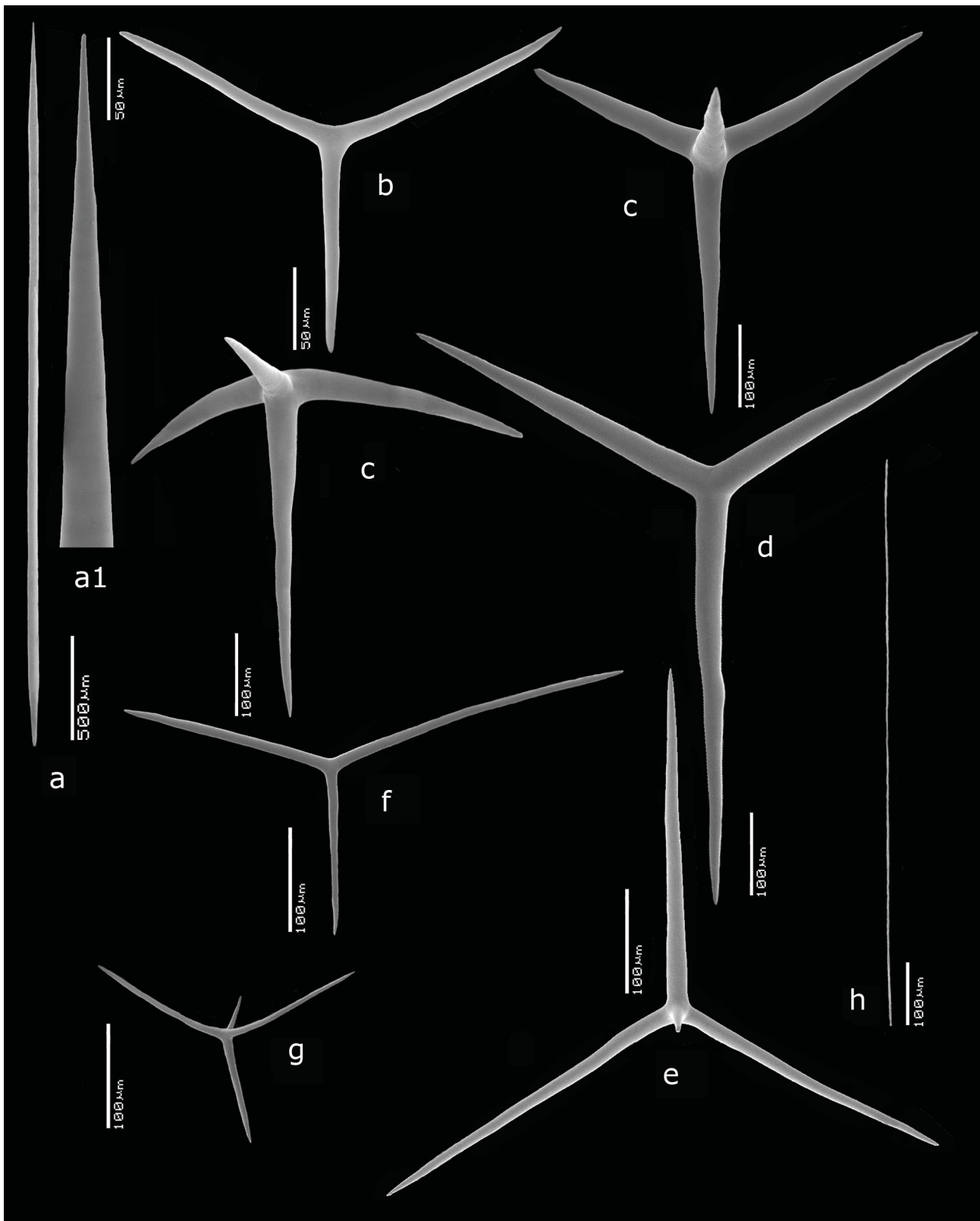


FIGURE 63. *Leucandrilla* aff. *intermedia* (Row, 1909), ZMA Por. 13482, from Gulf of Aqaba, a, giant diactine, a1, detail of ending of the same, b, cortical oxea, c, subcortical tetractines, d, large triactine, e, subatrial tetractine, f, atrial triactine, g, atrial tetractine, h, trichoxea (fragment).

Unfortunately, we were unable to obtain partial 28S sequence data. To investigate the likely position of the genus *Leucandrilla* in our phylogeny of Fig. 3, we obtained sequences of a *Leucandrilla* spec. (GenBank acc.nrs.

MF872768, MF872769, MF872770 and MF872771) from the Galapagos Islands. We included these in a separate analysis of the combined Galapagos and all other Calcaronea sequences, with the result that the Galapagos *Leucandrilla* grouped in the same clade with the above mentioned *Leucandra* sequences, at a low bootstrap value (42%). We do not show this result because we did not obtain Western Indian Ocean or Red Sea sequences of *Leucandrilla* to compare them with, but mention this examination to confirm that *Leucandrilla* and *Leucandra* are likely more closely related to each other than either is to other Calcaronea.

***Leucandrilla wasinensis* (Jenkin, 1908)**

Figs 64a–e, 65a–g.

Leucilla wasinensis Jenkin, 1908: 454, figs 104A–B.

Leucandra wasinensis; Dendy 1913: 24, pl. 2 fig. 5.

(Not: *Leuconia wasinensis*; Burton 1959: 181 = *Sycettusa* cf. *simplex*).

Material examined. ZMA Por. 11561, Seychelles, Amirantes, N of Poivre island, 5.7°S 53.3°E, depth 42–45 m, calcareous gravel bottom, 2.4 m Agassiz trawl, coll. R.W.M. van Soest, field nr. NIOP-E stat. 776/21, 31 December 1992.

Description. White, sycon-like sponge (Fig. 64a), with prominent fringe and hairy surface. Size 2 cm high, 1.2 cm in diameter, atrial lumen 1–2 mm in diameter. Consistency firm.

Aquiferous system. Leuconoid.

Skeleton. (Figs 64b–e) The cortical region (Figs 64b–c) consists of a layer of smaller triactines covering a layer of subcortical tetractines. The cortical skeleton is pierced by single giant diactines causing the hispidation. The main skeleton (Fig. 64b,d) contains a mass of large and small triactines, and some tetractines. The atrial skeleton (Fig. 64d) consists of smaller tri- and tetractines. The fringe (Fig. 64e) consists of a mixture of giant diactines, trichoxeas and sagittal tri- and tetractines.

Spicules. (Figs 65a–g) Triactines, tetractines, giant diactines, trichoxeas.

Large triactines (Fig. 65a), equiangular, usually slightly sagittal, actines 286–340–448 x 21–30.9–38 µm.

Smaller cortical and choanosomal triactines (Fig. 65b), 210–241–279 x 18–25.5–31 µm.

Smaller choanosomal and subatrial triactines (Fig. 65c), sagittal or irregular, unpaired actines 122–170–203 x 14–18.1–22 µm, paired actines 63–171–249 x 12–16.4–21 µm.

Large subcortical tetractines (Figs 65d), sagittal, unpaired actines 212–389–521 x 11–20.4–26 µm, paired actines 116–194–252 x 10–17.6–24 µm, apical actines 12–49–66 x 4–5.9–9 µm.

Small atrial tetractines (Figs 65e), sagittal, with curved paired actines, and straight or curved apical actines; unpaired actines 32–97–164 x 4–8.7–14 µm, paired actines 49–105–136 x 4–8.4–11 µm, apical actines 38–61–112 x 4–7.2–10 µm.

Trichoxeas (Fig. 65f), straight, thin, invariably broken in the slides, fragments 200–515 x 2–5 µm.

Giant diactines (Figs 65g), curved, endings tapering to sharp points, 1390–2072–2520 x 20–52.3–62 µm.

Distribution and ecology. Seychelles, Wasini Island off Kenya, Saya de Malha, on gravelly bottom at greater depth (>40 m). Burton (1959) reported *Leuconia wasinensis* from the South Arabian region (38 m), but he did not provide a description. Its identity was re-examined and the record is reassigned here, see below.

Remarks. The specimen described above resembles previous descriptions of Jenkin (1908) and Dendy (1913) in most details. Jenkin's material had the larger triactines up to 950 x 40 µm (in our material 448 x 38 µm). Likewise, the subcortical tetractines of Jenkin's specimen were larger, up to 700 x 28 µm (ours 521 x 26 µm), and also the atrial tetractines were considerably larger than ours. Dendy's (1913) description lacks detailed spicule measurements, but he admits that the spicules of his specimen were 'a good deal smaller' than Jenkin's. We assume here that spicule sizes are subject to variation.

Burton (1959) recorded this species (as *Leuconia*), but after re-examination this was found to be very similar to *Sycettusa simplex* (Jenkin, 1908), see the Remarks of that species below.

Unfortunately, our attempt to obtain partial 28S sequences of this species failed.

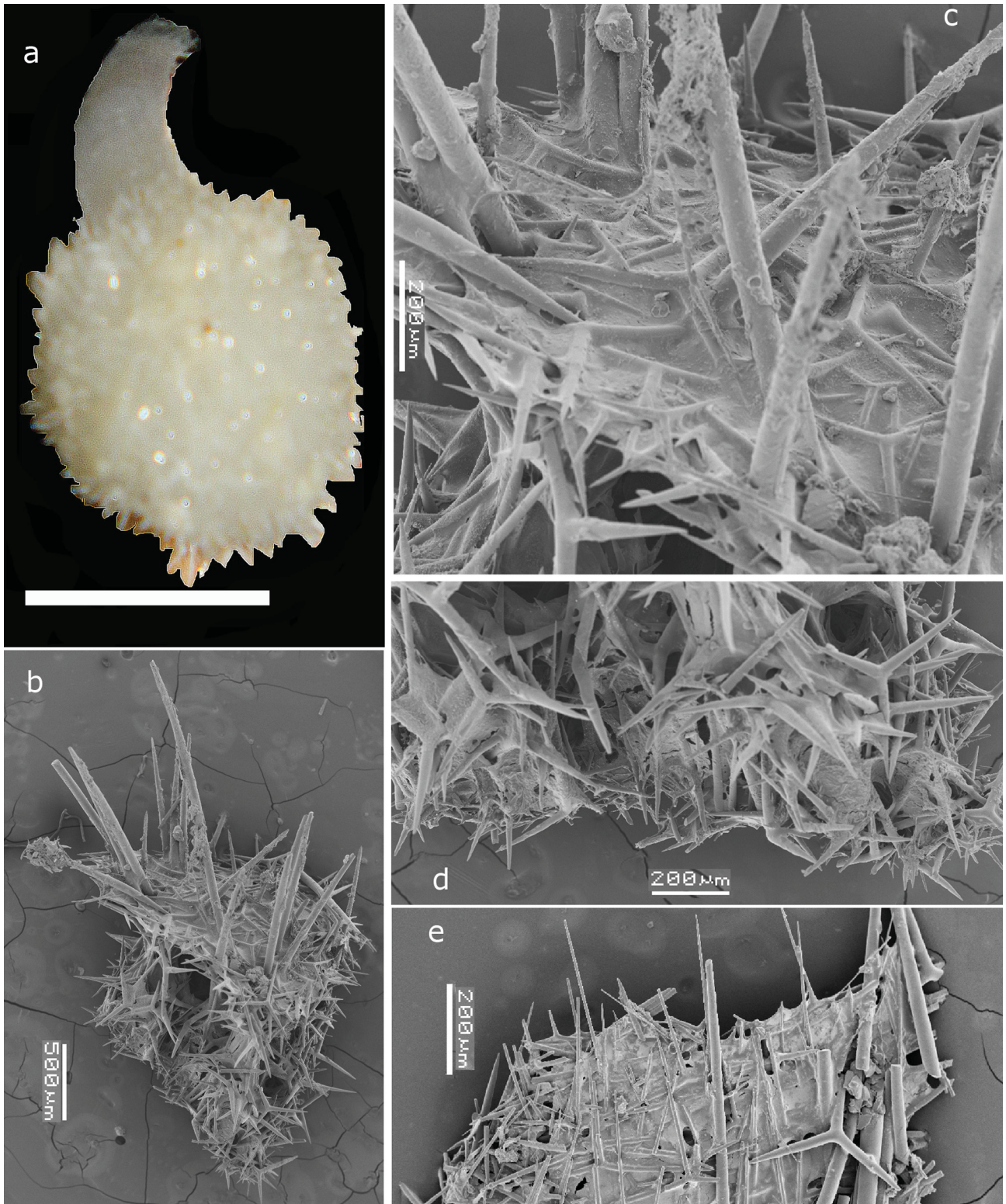


FIGURE 64. *Leucandrilla wasinensis* (Jenkin, 1908), ZMA Por. 11561, from the Seychelles, a, preserved habitus (scale bar = 1 cm), b–e, SEM images of the skeleton, b, cross section, c, view of the surface skeleton, d, view of the atrial skeleton, e, skeleton of the upper-inner rim of the fringe.

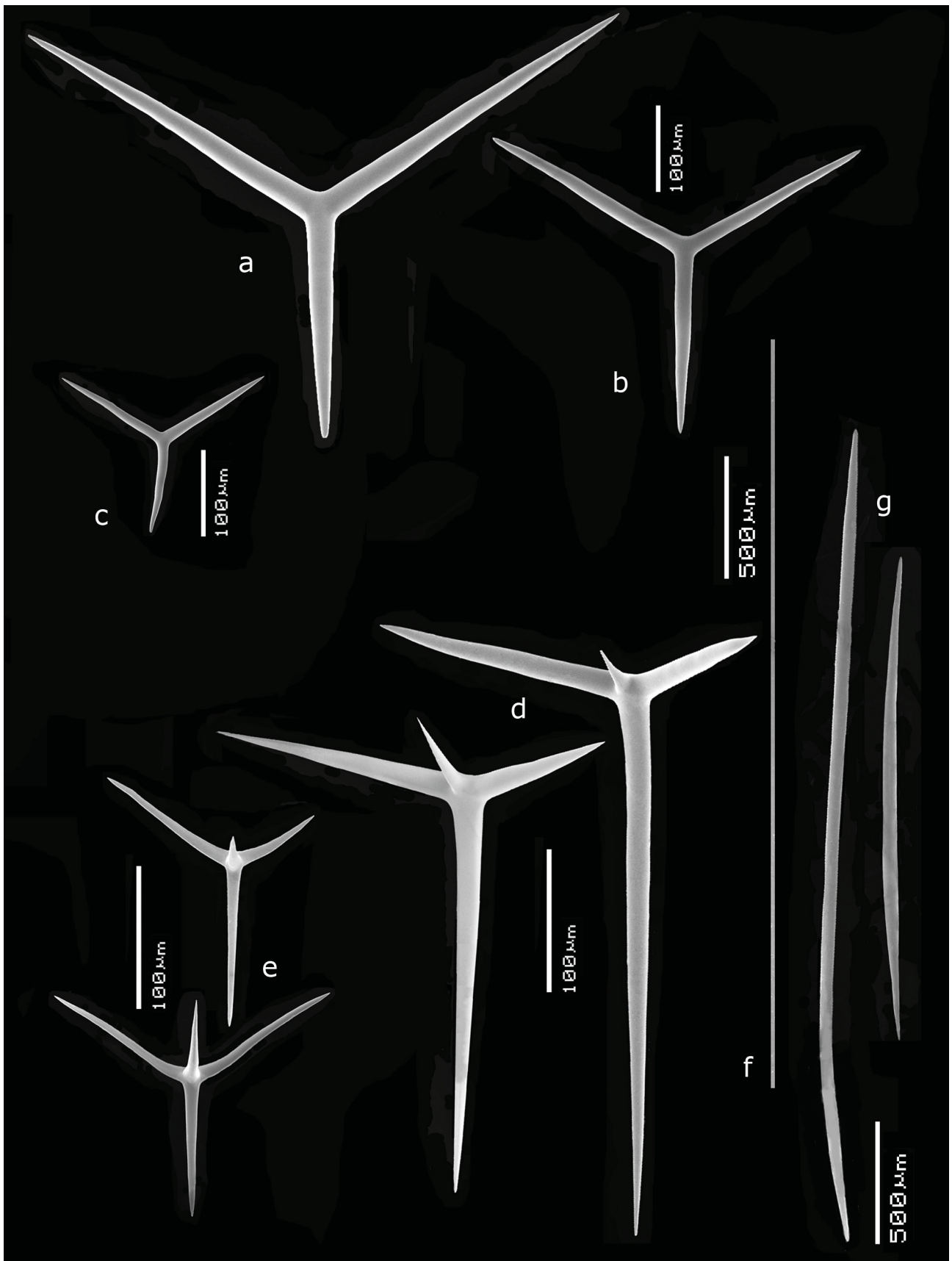


FIGURE 65. *Leucandrilla wasinensis* (Jenkin, 1908), ZMA Por. 11561, from the Seychelles, SEM images of the spicules, a, large triactine, b, smaller cortical triactine, c, smaller choanosomal triactine, d, subcortical large tetractines, e, atrial tetractines, f, trichoxea (fragment), g, giant diactines.

Family Heteropiidae Dendy, 1893

Genus *Grantessa* Von Lendenfeld, 1885

Grantessa woerheidei sp.nov.

Figs 66a–f, 67a–g

Material examined. Holotype, RMNH Por. 9586, Saudi Arabia, Jeddah, near Thuwal, Abu Gishaa, 22.255194°N 39.025639°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. THU06/JED081, 9 November 2014.

Description. Extremely ‘hairy’ sycon-like ovoid sponge (Figs 66a–b), whitish in situ, light beige in preservation. Size 2 cm high, 0.5 cm in diameter (1 cm if protruding diactines are included). Consistency compressible but firm.

Aquiferous system. Syconoid.

Skeleton. (Figs 66c–f) Articulate, with radiating structure following the syconoid aquiferous system. The wall of the sponge is pierced almost for its entire thickness by long giant diactines, and these protrude beyond the surface for a considerable distance. From the periphery to the atrial cavity there is first a thin cortical layer of small triactines, overlying a layer of pseudosagittal triactines, with the unpaired and short paired actine tangential to the surface and the long paired actine directed inwards. Next, the choanosomal skeleton (Figs 66c–d) consists of aligned tracts of sagittal tubar triactines with the unpaired actines directed outwards and the paired actines similarly aligned parallel to the cortical and atrial surfaces. Below this, the subatrial skeleton is formed by triactines similar to the tubar triactines but with unpaired actines elongated, also directed outwards. Finally, the atrial skeleton is formed by the basal triadial system of tetractines, with their apical actines protruding far into the atrial cavity (Fig. 66d). Although there is not a separate fringe, the oscular opening is surrounded by protruding diactines (Fig. 66e) even longer than those of the main body, and these also form bundles, which give the opening a star-like appearance. The oscular rim is strengthened by rows of triactines (Fig. 66f)

Spicules. (Figs 67a–g) Diactines, triactines, pseudosagittal triactines, tetractines.

Giant diactines (Figs 67a,a1), long, straight, varying in thickness from trichoxea-like thin diactines to thickly fusiform longer and shorter spicules, with endings varying from thinly sharply tapering to lance-shaped, those protruding from the main body 700–2791–4900 x 4–25.8–33 µm, the oscular diactines are at least 6–7 mm x 3–20 µm.

Triactines of the oscular rim (Fig. 67b), sagittal, rather strongly recurved, only a few could be measured, actines 70–130 x 7–10 µm.

Triactines of the cortical skeleton (Figs 67c), slightly sagittal, actines 62–111–145 x 5–7.6–9 µm.

Pseudosagittal triactines (Figs 73d), of variable shape but always clearly distinct from other triactines by having all actines of different length and usually partially curved, unpaired actines 86–112–132 x 5–6.2–7.5 µm, long paired actines 92–189–244 x 5–6.0–7.5 µm, short paired actines 36–48–65 x 5–5.7–7 µm.

Tubar triactines (Figs 67e), sagittal, equiangular, unpaired actines 110–124–146 x 5–7.6–11 µm, paired actines 84–125–193 x 5–7.1–10 µm.

Subatrial triactines (Fig. 67f), sagittal, equiangular, with unpaired actine longer than paired actines, measuring 195–223–285 x 5–7.7–11 µm, paired actines 63–110–132 x 4–6.4–10 µm.

Atrial tetractines (Figs 67g), with slightly curved actines, often with apical actines longest; unpaired actines 102–134–186 x 4–5.6–8 µm, paired actines 99–144–180 x 4–5.3–7 µm, apical actines 46–155–345 x 3–5.3–10 µm.

Distribution and ecology. Saudi Arabia, Red Sea, from shallow-water reef overhangs.

Etymology. Named after Professor Gert Wörheide, München, to acknowledge his important contributions to Calcarea systematics.

Remarks. On paper this species appears close to Southeast Australian *Grantessa hirsuta* (Carter, 1886) (originally as *Hypograntia*), as redescribed by Dendy (1893a) and Burton (1963: 461). Unfortunately there are no images of this species published so far. From the description it is clear that it is a small cylindrical sponge (about 2 cm high) with hispid surface and apical fringe. However, the details provided by the latter two authors show several distinct differences with our new species: (1) the diactines protruding from the surface are given as 500–1000 x 14 µm, against up to 7000 x 35 µm in our specimen, (2) the apical actines of the atrial tetractines are given as up to 100 x 6, against up to 345 x 10 µm in our specimen, (3) the articulated skeleton is described as being irregular,

whereas our specimen has a very regular tubar skeleton. The lack of differentiation in the various kinds of tri- and tetractines provided in these descriptions makes it hard to be certain of the value of these differences. At least, the length of the diactines and the atrial apical actines provide quite a different aspect in the skeletal structure. The geographic distance and temperature discrepancy between temperate SE Australian waters and the tropical Red Sea adds a further argument for specific distinctness.

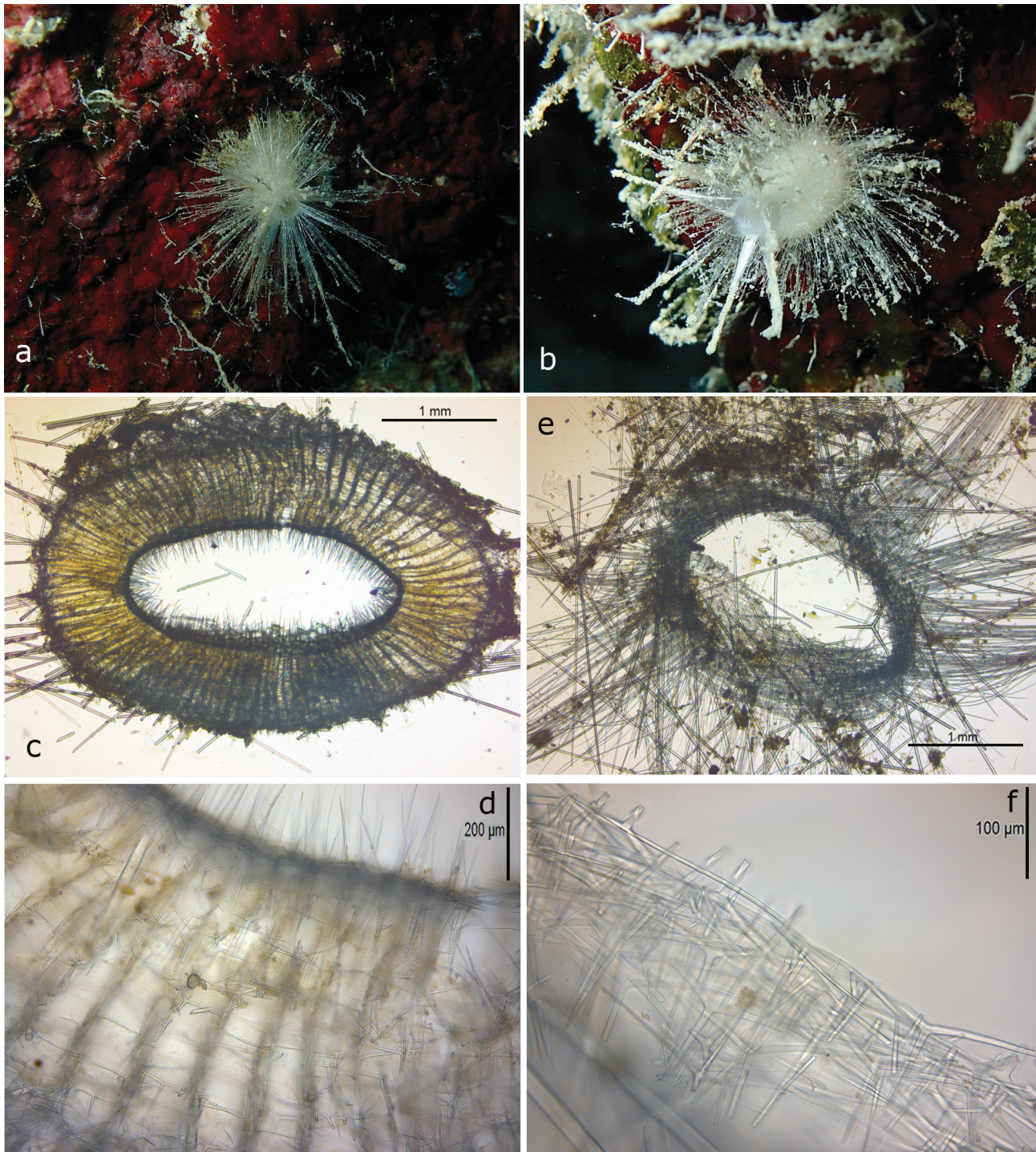


FIGURE 66. *Grantessa woerheidei* sp.nov., holotype RMNH Por. 9586 from Saudi Arabia, Red Sea, a–b, habitus in situ from above and from the side (photos N.J. de Voogd), c–f, light microscopic images of skeleton, c, cross section, d, detail of c, showing choanosomal and atrial region, e, view of oscular region, f, detail of oscular rim.

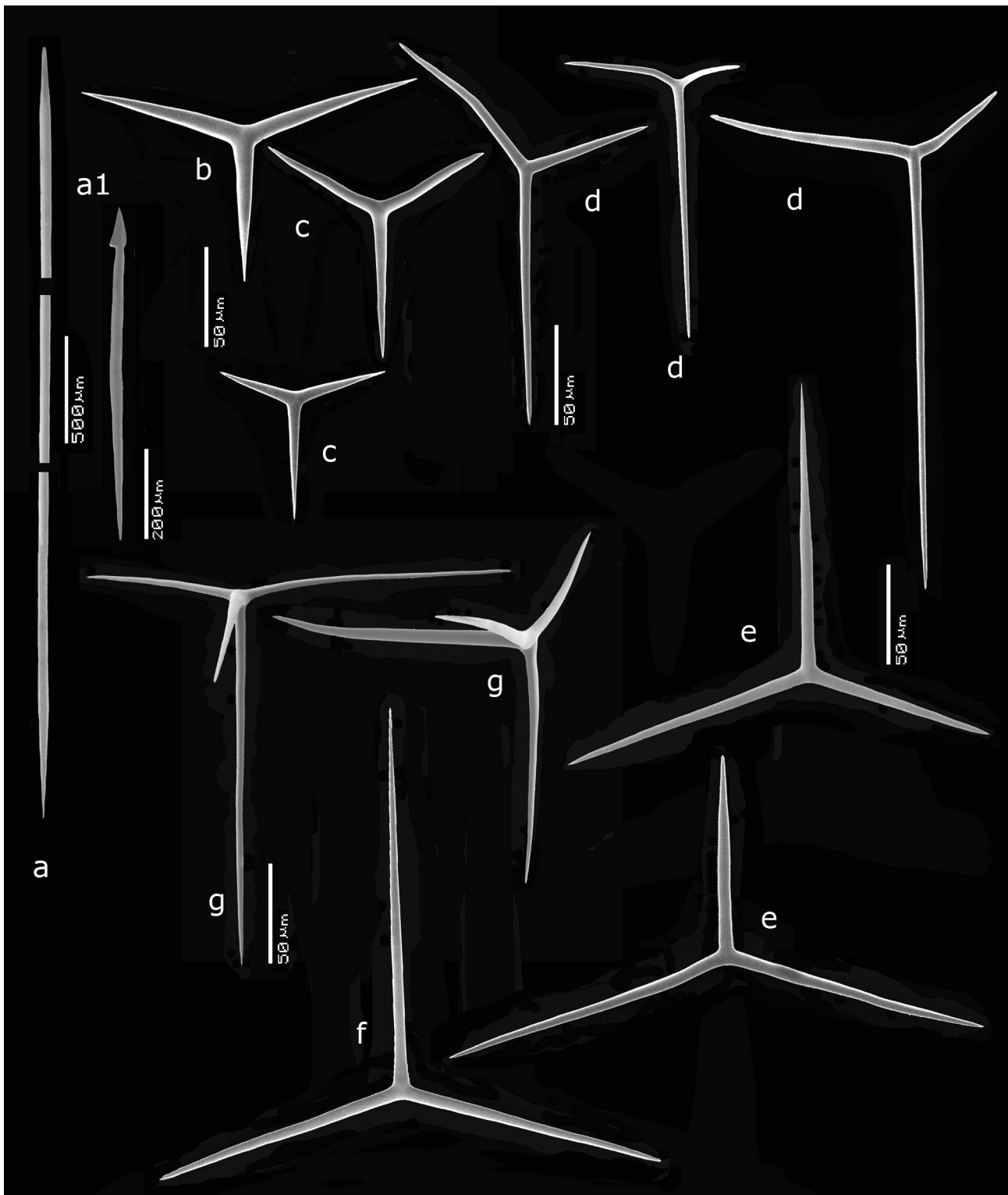


FIGURE 67. *Grantessa woerheidei* **sp.nov.**, holotype RMNH Por. 9586 from Saudi Arabia, Red Sea, SEM images of the spicules, a, giant diactine with pointed apices, a1, smaller diactine with lance head, b, triactine of the oscular rim, c, triactines of the cortical skeleton, d, pseudosagittal triactines of the subcortical region, e, tubar triactines, f, subatrial triactines, g, atrial tetractines.

There is a possibility that our new species was previously recorded from the Gulf of Aden by Burton (1959) under the name *Grantessa sycilloides* (Schuffner, 1877). We reexamined Burton's specimen (Murray Expedition station 24, nr 538) in 2004 and from our notes found this to be close in spiculation: giant diactines protruding from the surface, cortical skeleton of small triactines, an articulate main skeleton of pseudosagittal and sagittal triactines,

and atrial skeleton of tetractines. In alcohol the specimen was brownish, shaggy. It is certainly unlike *Sycortis sycilloides* Schuffner, 1877, as this is largely smooth and does not have atrial tetractines. Schuffner's species could be a junior synonym of *Sycettusa stauridia* (see below), but this remains undecided.

The genus *Grantessa* is large. In our recent paper on Indonesian Calcarea, in which we described two new species, we discussed most of the species occurring in the Indo-West Pacific. We refer to this paper (pp. 82–86) for the more distantly distributed species. The two Indonesian species (*G. borojevici* Van Soest & De Voogd, 2015 and *G. tenhoveni* Van Soest & De Voogd, 2015) are clearly distinct from *G. woerheidei* **sp.nov.** in having a smooth surface (with only small diactines in the cortical region) and both comprise coalescent groups of individuals. Additionally, they differ in details of their spiculation. The small diactines mentioned for the Indonesian species also occur in the widespread, smooth-surfaced *G. intusarticulata* (Carter, 1886) (originally as *Hypograntia*) and the South African *G. rarispinosa* Borojević, 1967. The latter two species lack tetractines. *G. ramosa* (Haeckel, 1872) (originally as *Sycandra*) as described by Borojević (1967, p. 204) from South Africa forms a group of coalescent individuals and has sagittal triactines with long swollen unpaired actines and tetractines likewise with swollen apical actines. No other *Grantessa* species are known from the region.

We obtained a partial 28S sequence of this specimen. In our Calcarea phylogeny of Fig. 3, which included a *Grantessa* cf. *intusarticulata* sequence downloaded from the Sponge Barcode Project, *Grantessa woerheidei* **sp.nov.** ended up in a mixed larger clade quite close to Indonesian *Uteopsis argentea* (Poléjaeff, 1883), away from *Grantessa* cf. *intusarticulata*. In a trimmed alignment of three identical *Uteopsis argentea* sequences and one *Grantessa woerheidei* sequence of 428 sites, only 5 sites were found to be different, indicating that the two are inexplicably close. Voigt *et al.* (2012) already found that the family monophyly of Heteropiidae could not be retrieved resulting in two Heteropiidae groups separated by some Jenkinidae. Clearly, more taxa are needed to sort out the relationships of *Grantessa*.

Genus *Sycettusa* Haeckel, 1872

Sycetta (*Sycettusa*) Haeckel, 1872: 236

? *Grantilla* Row, 1909: 187; Borojević *et al.* 2002b: 1176.

Remarks. According to the Systema Porifera, chapter on the order Leucosolenida by Borojević *et al.* 2002b, *Sycettusa* Haeckel, 1872 and *Grantilla* Row, 1909, differ only in the presence in the latter of pseudosagittal tetractines in addition to pseudosagittal triactines. We borrowed two slides of the type specimen of *Grantilla quadriradiata* Row, 1909 from the collections of the Natural History Museum, London, BMNH 1912.2.1.8a. This species is the type and only member of the genus *Grantilla* recognized by Borojević *et al.* 2002b. The slides consisted of sections and dissociated spicule mounts. Remarkably these did not contain a single recognizable subcortical pseudosagittal tetractine, but instead had only pseudosagittal triactines (called 'prochiacts' by Row). There was not a single tetractine in the borrowed material, despite its alleged occurrence in the extensive description of Row (1909, p. 198). We studied a number of *Sycettusa* specimens answering to the description of *Grantilla hastifera* Row, 1909, and these are not separable from the studied type material of *Grantilla quadriradiata*. We propose to consider *Grantilla* a junior synonym of *Sycettusa* because even if Row's material ultimately will be found to contain a few quadriradiate pseudosagittal spicules, their rarity and overall similarity with *Sycettusa hastifera* is hardly a difference meriting generic distinction.

Sycettusa was erected by Haeckel (1872), as a subgenus of his genus *Sycetta*, for type species *Sycetta stauridia* Haeckel, 1872, but subsequently he refrained from using the combination. He did use a further combination *Sycothamnus stauridia* in his confusing artificial system as a 'generische Individualität', a remnant from his 1870 Prodomus, which is hopefully to be suppressed in the near future as a source for named sponge taxa.

A further issue in the genus *Sycettusa* is the lack of differentiation in the complement of the spicules and their sizes and shapes in many forms that differ distinctly in habitus (color, shape, size, oscular openings and protruding diactines). Apparently, overall shape is an important marker for species recognition.

We obtained several partial 28S sequences of members of the genus, some of which tend to support specific distinction of specimens showing very little differentiation in their spicule complement. The genus appears to be non-monophyletic in our phylogeny of Fig. 3, with *Sycettusa zanzibaris* (Jenkin, 1908) and New Caledonian *S. tenuis* Borojević & Klautau, 2000 grouped with *Grantessa* cf. *intusarticulata*, separated from a predominantly Red

Sea group of *Sycettusa* species by *Grantessa woerheidei*, and *Uteopsis* and *Ute*. As argued above, the small number of Calcareous partial 28S rRNA sequences, may be responsible for this inconsistent result. Nevertheless, it may be possible that *Sycettusa* is genuinely non-monophyletic.

***Sycettusa hastifera* (Row, 1909)**

Figs 68a–g, 69a–f, 70a–f

Grantilla hastifera Row, 1909: 200, pl. 19 figs 3–4, text fig. 3.

? *Grantilla quadriradiata* Row, 1909: 198, pl. 19 fig. 2, text fig. 2.

Grantessa hastifera; Dendy 1913: 19, pl. 2 fig. 6; Dendy 1916: 81, pl. 1 fig. 2, pl. 2 fig. 7; Borojević 1967: 210, fig. 17.

Material examined. RMNH Por. 9587, Saudi Arabia, Jeddah, near Thuwal, Abu Gishaa, 22.255194°N 39.025639°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. THU06/JED082, 9 November 2014; RMNH Por. 9644, Saudi Arabia, Jeddah, near Thuwal, Um Alsawi, 22.239306°N 38.985139°E, scuba, coll. N.J. de Voogd, field nr. THU08/JED144, 11 November 2014; RMNH Por. 9645, Saudi Arabia, Jeddah, near Thuwal, Um Alsawi, 22.239306°N 38.985139°E, scuba, coll. N.J. de Voogd, field nr. THU08/JED145, 11 November 2014; RMNH Por. 9659, Saudi Arabia, Jeddah, near Thuwal, Fsar, 22.249417°N 39.002333°E, scuba, coll. N.J. de Voogd, field nr. THU09/JED159, 11 November 2014; ZMA Por. 13421, Israel, Gulf of Aqaba, on pillar of containerport, depth 5 m, scuba, coll. M. Wunsch, field nr. AQ70, 5 July 1998; ZMA Por. 13422, Israel, Gulf of Aqaba, Marsa Bareika, depth 20 m, in cave, scuba, coll. M. Wunsch, field nr. RM227, 25 July 1998; ZMA Por. 13429, Israel, Gulf of Aqaba, Shark Observatory, depth 14 m, in cave, scuba, coll. M. Wunsch, field nr. RM241, 26 July 1998; ZMA Por. 13443, Israel, Gulf of Aqaba, on pillar of containerport, depth 7 m, scuba, coll. M. Wunsch, field nr. AQ73, 5 July 1998; ZMA Por. 13448, Israel, Gulf of Aqaba, Canyon, cryptic habitat, depth 10 m, scuba, coll. M. Wunsch, field nr. AQ137, 14 July 1998; ZMA Por. 13508, Israel, Gulf of Aqaba, North Pinnacle, depth 8 m, in cave, scuba, coll. M. Wunsch, field nr. AQ56, 4 July 1998; ZMA Por. 13509, Israel, Gulf of Aqaba, North Pinnacle, depth 17 m, in cave, scuba, coll. M. Wunsch, field nr. AQ33, 4 July 1998; ZMA Por. 10524, Seychelles, E of Bird Island, 3.7333°S 55.2333°E, depth 45 m, dredge, coll. R.W.M. van Soest, field nr. NIOP-E stat. 719/08, 20 December 1992; ZMA Por. 11563, Seychelles, Amirantes, St. François Atoll, Île Bijoutier, 7.0833°S 52.7333°E, reef, depth 6–18 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 792/16, 5 January 1993.

Description. Cylindrical, hairy sponges (Figs 68a–f, 69a,c), usually hanging down from ceilings or walls of reef caves. Size varies between 1 and 3 cm high, diameter 2–10 mm (protruding diactines included). Colors in situ varying from whitish, pale greenish, to greyish transparent; in preservation (Figs 69b,d) they are light beige. Oscules are slightly constricted, lack a distinct fringe, but have a dense collar of long diactines and trichoxeas (Figs 68f, 69c), which form bundles radiating outwards from the oscule (Fig. 69e). Consistency soft.

Aquiferous system. Syconoid.

Skeleton. (Figs 68g, 69e–f) Inarticulate, with the choanosomal region supported by the longer paired actines of pseudosagittal triactines and the unpaired actines of subatrial triactines. The cortical skeleton consists of large regular or slightly sagittal triactines carried by the shorter paired actines of the pseudosagittal triactines. Giant diactines are protruding far outwards from the cortex (Fig. 69e) and penetrate deeply into the choanosomal skeleton contributing to the inarticulate triactine skeleton. The (sub-)atrial skeleton consists of the paired actines of subatrial triactines (Fig. 69f) and smaller sagittal or oxborn-shaped triactines.

Spicules. (Figs 70a–f) Giant diactines, trichoxeas, cortical triactines, pseudosagittal triactines, subatrial triactines, atrial triactines.

Giant diactines (Figs 70a), sharply pointed or with lance-head ending, 240–903–2040 x 10–26.9–36 µm.

Trichoxeas (Fig. 70b), invariably broken, fragments of all lengths up to 1048 x 3 µm.

Cortical triactines (Fig. 70c), usually more or less equiradiate and equiangular, variable in actine length within and among specimens, 181–221–310 x 14–16.1–30 µm.

Pseudosagittal triactines (Fig. 70d), especially variable in thickness of the actines, long paired actine straight, 246–398–480 x 14–24.2–40 µm, short paired actine curved 105–176–285 x 13–20.7–29 µm, unpaired actine straight or slightly curved, 107–177–325 x 14–22.4–32 µm.

Subatrial triactines (Fig. 70e), mostly strongly sagittal, varying from almost T-shaped to widely curved paired actines, with unpaired actine straight, tapering to thin sharp ends or occasionally bluntly rounded; unpaired actines

306–436–620 x 17–31.1–46 μ m, paired actines 166–239–318 x 18–27.2–45 μ m.

Atrial triactines (Figs 70f), sagittal, often with curved paired actines; unpaired actines 68–141–201 x 7.5–10.9–15 μ m, paired actines 72–147–215 x 9–10.7–15 μ m.

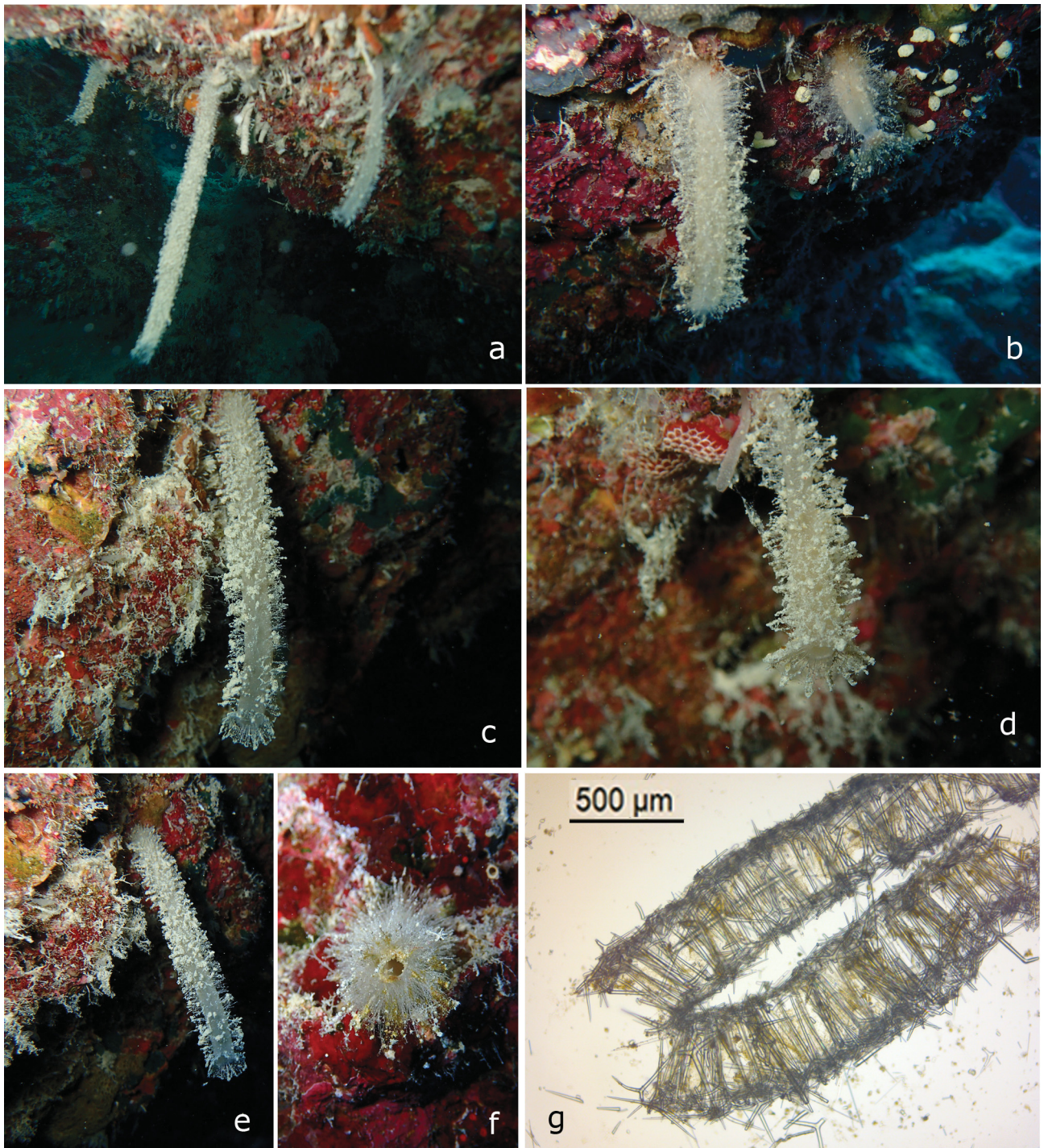


FIGURE 68. *Sycettusa hastifera* (Row, 1909), a–f, habitus in situ of various specimens from Saudi Arabia (photos N.J. de Voogd), preserved as RMNH Por. 9644, 9645 and 9659, g, light microscopic photo of cross section of RMNH Por. 9659.

Distribution and ecology. Red Sea, Seychelles, Western India, South Africa, in caves and other cryptic habitats, 5–45 m depth; records from the Southwest Atlantic (Lanna & Klautau 2010) probably concern a similar but different species of *Sycettusa*.

Remarks. As indicated above, we tentatively consider *Grantilla quadriradiata* Row, 1909 a synonym of *S. hastifera* based on examination of several slides (sections and spicule mounts) of the holotype incorporated in the

collections of the Natural History Museum, London, under reg.nr. BMNH 1912.2.1.8a. There are no tetractines in the slides, so even if they are present in other parts of the type material, they are obviously a minor complement, probably derived from the usual pseudosagittal triactines. The *G. quadriradiata* spicules were at the larger part of the variation of length and thickness, but fell within it. There are no clear differences with the dozen specimens of *S. hastifera* present in our collection.

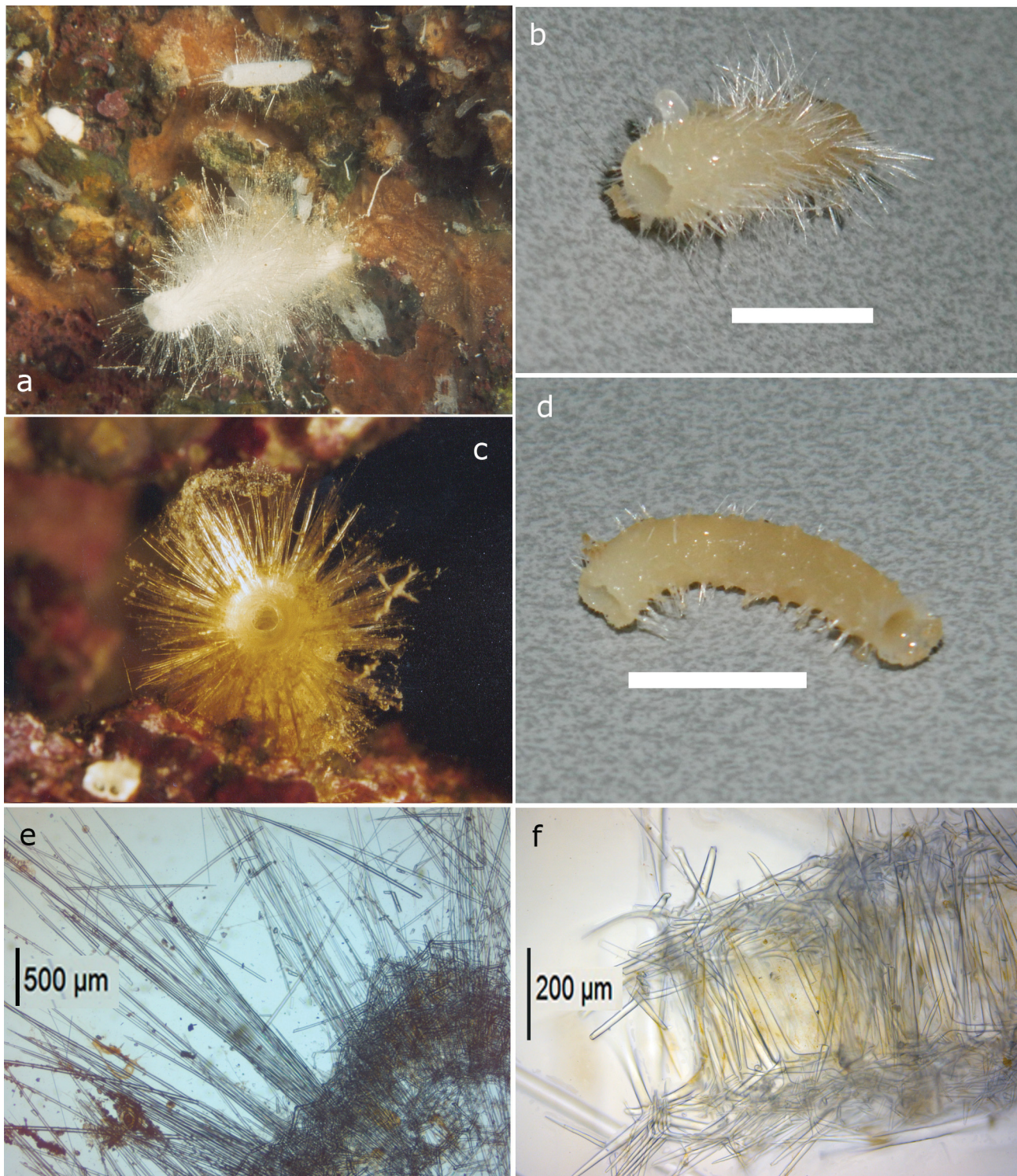


FIGURE 69. *Sycettusa hastifera* (Row, 1909), a–d, habitus of specimens from Israel, Gulf of Aqaba, a, ZMA Por. 13429 in situ (photo M. Wunsch), b, ditto preserved, c, ZMA Por. 13508 in situ (photo M. Wunsch), d, ditto preserved, e, light microscopic photo of oscular region of ZMA Por. 13421, f, light microscopic photo of cross section of ZMA Por. 13429.

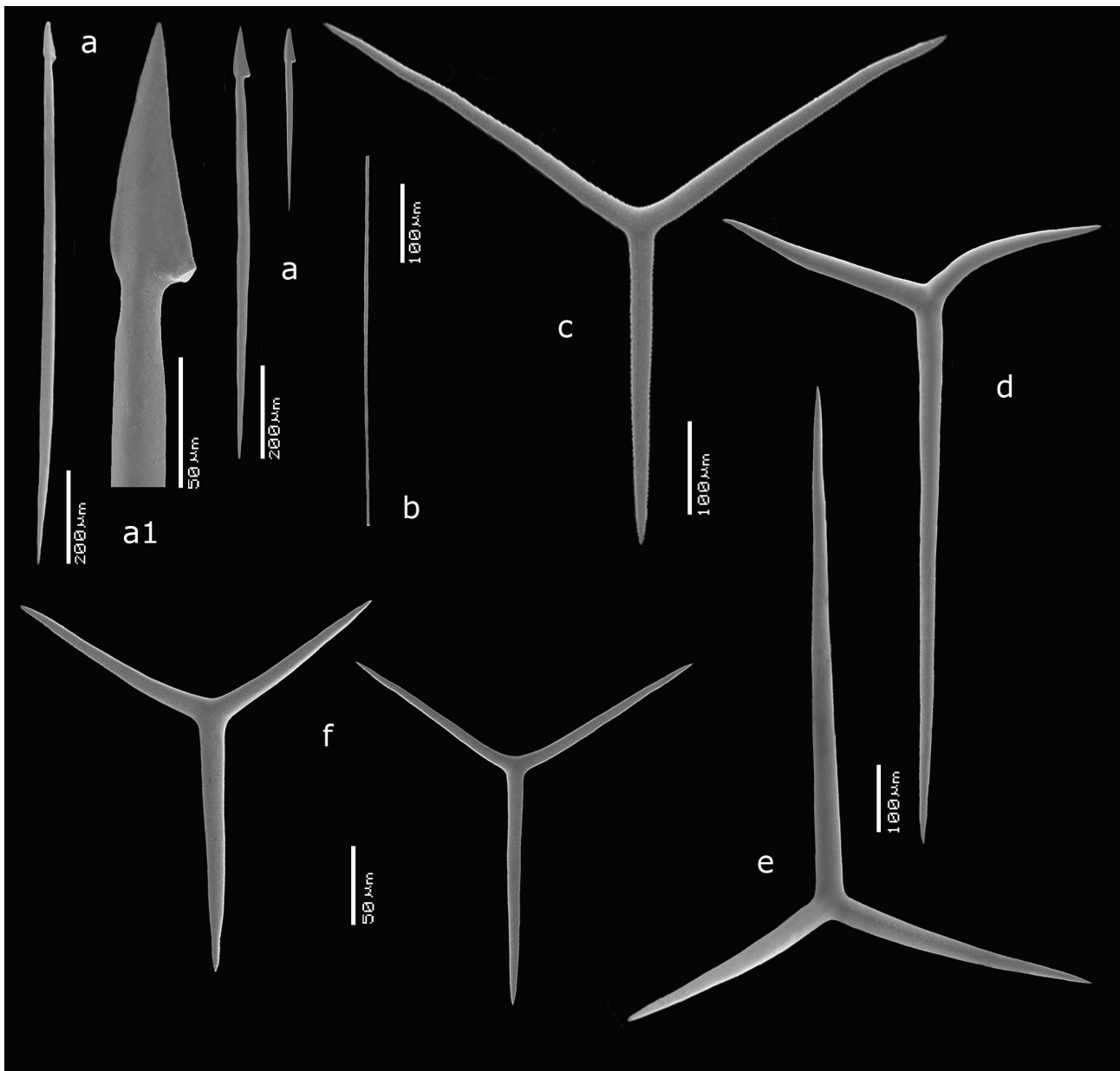


FIGURE 70. *Sycettusa hastifera* (Row, 1909), ZMA Por. 13421 from Gulf of Aqaba, a–f, SEM images of the spicules, a, lance-head diactines, a1, detail of lance-head, b, broken trichoxea, c, cortical triactine, d, pseudosagittal triactine, e, sagittal triactine, f, atrial triactines.

Dendy (1913, 1916) assigned *Grantilla* Row, 1909 (with species *G. quadriradiata* and *G. hastifera*) to *Grantessa* Von Lendenfeld, 1885, but that genus has been redefined by Borojević *et al.* 2000, 2002b to have an articulate skeleton. Row's species and our specimens have clearly inarticulate skeletons and thus answer to *Sycettusa* Haeckel, 1872 as redefined by Borojević *et al.* 2002b.

Three sequences available to us, two of our own and one downloaded from the Sponge Barcode Project site, all three from the Red Sea, grouped together in the same clade in the phylogeny of Fig.3.

There are several further species of *Sycettusa* in our material, which will be described below and their differences with *S. hastifera* will be discussed in the Remarks of those species below.

Sycettusa hirsutissima sp.nov.

Figs 71a–d, 72a–g

Material examined. Holotype, RMNH Por. 10004, Saudi Arabia, Jeddah, near Thuwal, Tahlah, 22.25725°N 38.880917°E, scuba, coll. N.J. de Voogd, field nr. THU14/JED211, 13 November 2014.

Paratype, RMNH Por. 9588, Saudi Arabia, Jeddah, near Thuwal, Abu Gishaa, 22.255194°N 39.025639°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. THU06/JED083, 9 November 2014.

Description. Densely hairy tubes (Figs 71a–b), hanging down, from reef walls. Color yellow or orange below a thick pelt of diactines. In preservation they become dark grey. Size up to 8 cm high, 0.5–1.5 cm in diameter. Consistency firm.

Aquiferous system. Syconoid.

Skeleton. (Figs 71c–d) Inarticulate with cortex of triactines, carried by the unpaired and shorter actines of pseudosagittal triactines. Choanosomal skeleton consists of the longer actines of the subcortical pseudosagittal triactines and the unpaired actines of sagittal subatrial triactines. Atrial skeleton consists of smaller sagittal triactines.

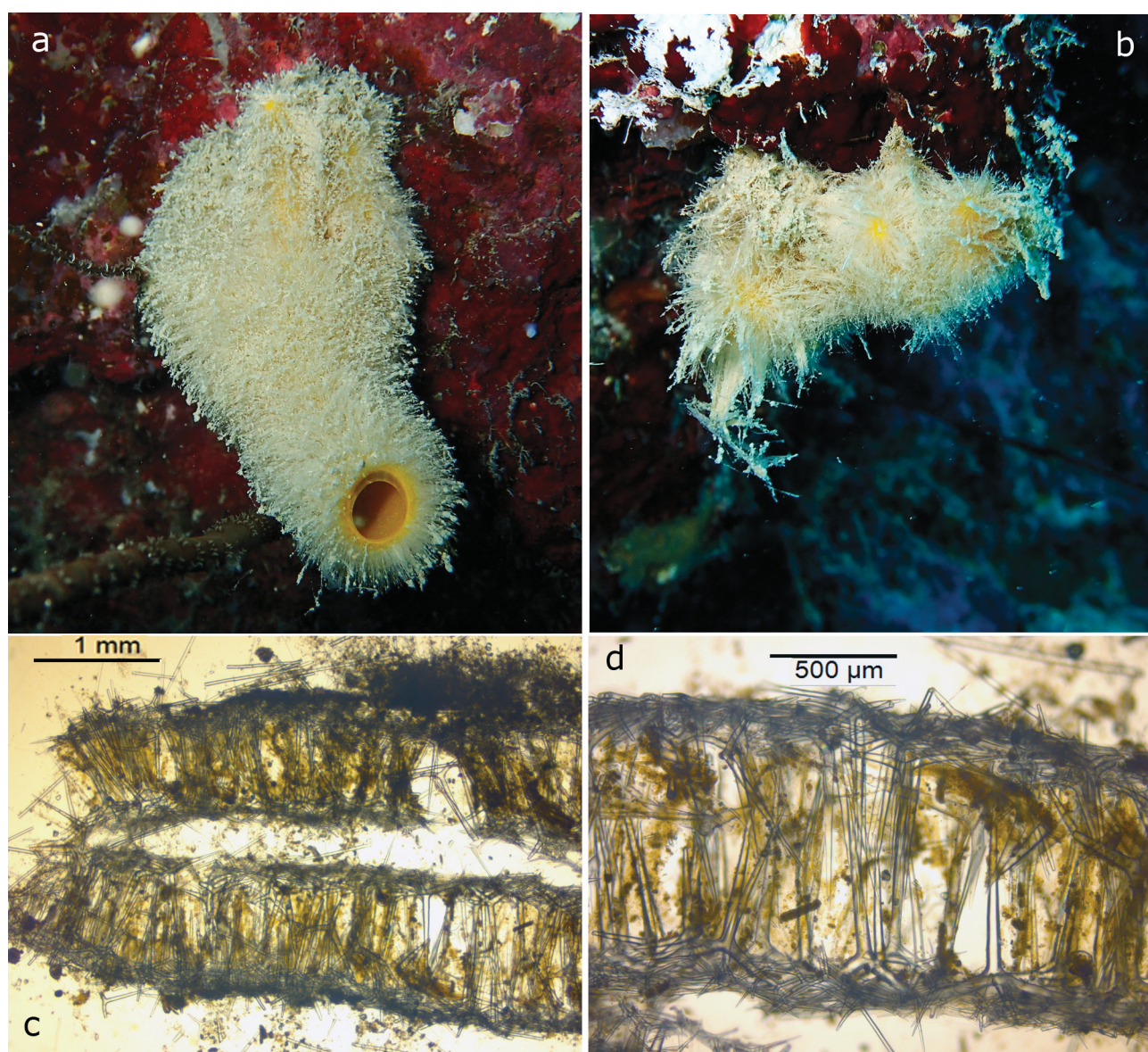


FIGURE 71. *Sycettusa hirsutissima* sp.nov., a, holotype RMNH Por. 10004, in situ on the reef off Jeddah, Saudi Arabia (photo N.J. de Voogd), b, paratype RMNH Por. 9588, ditto, c, light microscopic image of cross section of holotype, d, detail of c.

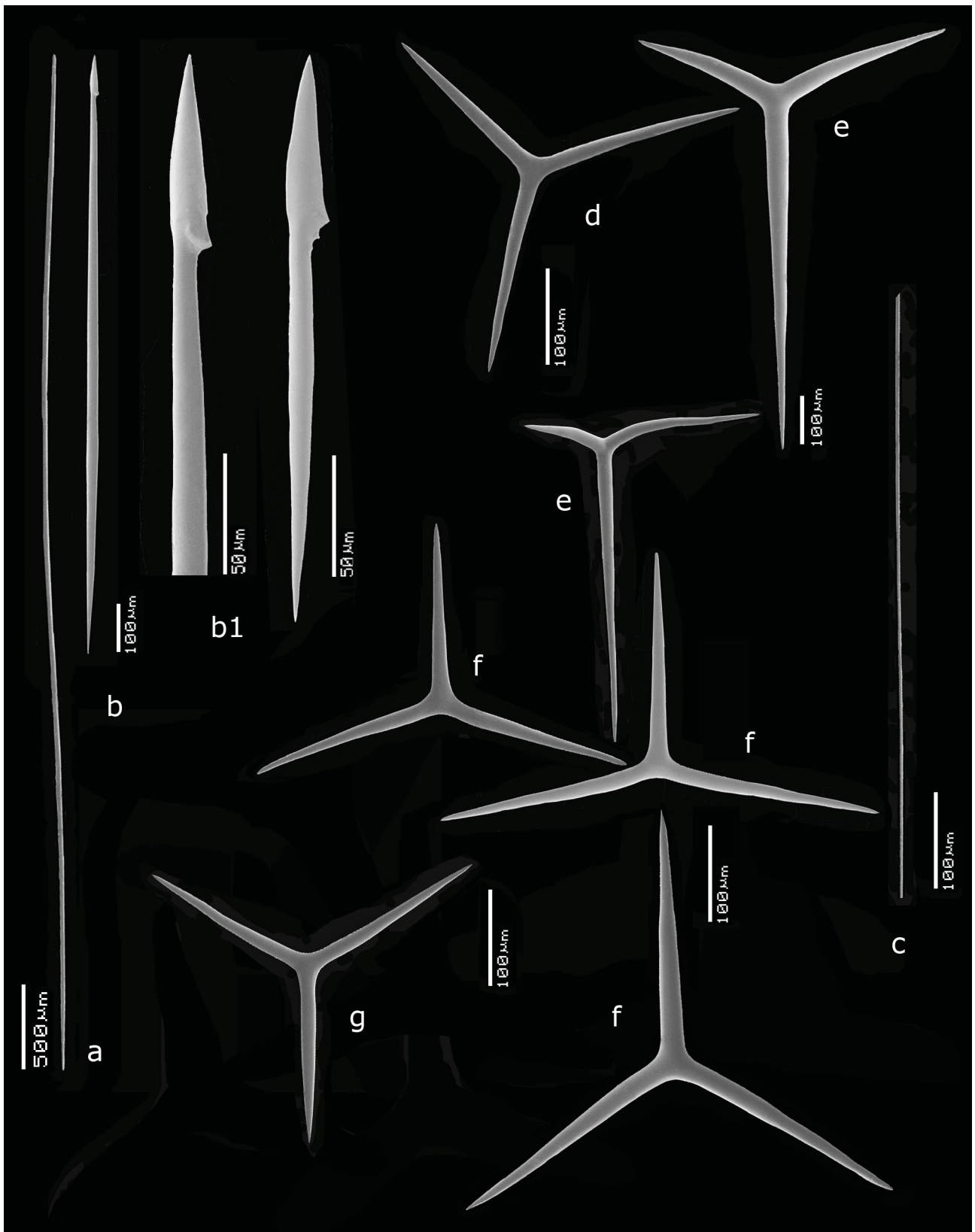


FIGURE 72. *Sycettusa hirsutissima* **sp.nov.**, holotype RMNH Por. 10004, a–g, SEM images of the spicules, a, long giant diactine, b, lance-headed giant diactines, b1, detail of lance-head, c, broken trichoxea, d, cortical triactine, e, pseudosagittal triactines, f, subatrial sagittal triactines, g, atrial triactine.

Spicules. (Figs 72a–g) Diactines, trichoxeas, cortical triactines, subcortical pseudoaagittal triactines, subatrial triactines, atrial triactines.

Diactines (Figs 72a–b), consisting of two types, long thin with sharp points (Fig. 72a), often fragmented, 1200–2213–3200 x 15–21.1–33 µm, and a shorter type with lance head endings of variable length and thickness (Figs 72b,b1), 336–1179–2110 x 12–20.3–30 µm.

Trichoxeas (Fig. 72c), invariably broken into smaller pieces, 540–1413–2940 x 2–2.9–3.5 µm.

Cortical triactines (Fig. 72d), almost regular or slightly sagittal, 171–202–261 x 10–16.0–18 µm.

Pseudosagittal triactines (Figs 72e), longest actine 420–582–738 x 24–31.3–43 µm, shorter actine 225–294–383 x 23–29.4–40 µm, unpaired actine 162–207–299 x 21–28.8–42 µm.

Subatrial triactines (Figs 72f), variably with longer and shorter unpaired actines and flat-angled or acute-angled paired actines, unpaired actines 282–490–530 x 282–36.6–52.5 µm, paired actines 162–258–375 x 14–31.6–46 µm.

Atrial triactines (Fig. 72g), slightly sagittal, 81–158–231 x 7–13.1–16 µm.

Distribution and ecology. Saudi Arabian Red Sea, on overhangs in shallow water.

Etymology. *Hirsutus* (L.) means hairy, rough, referring to the ‘pelt’ of long protruding bundles of diactines. We use the superlative of *hirsutus* to emphasize the extreme hairiness.

Remarks. The new species is close to *S. hastifera* in overall appearance and in spicule complement. However, the two specimens are extremely and densely hairy, unlike the dozen *S. hastifera* specimens we had at our disposal, which have the protruding diactines much less dense. In the new species, the body wall underneath the pelt of diactines is barely visible and has a yellow color, while it is always clearly visible and greyish or greenish white in *S. hastifera*. In contrast to *S. hastifera* the sizes (length and thickness) of the longest actine of the pseudodosagittal triactines of our new species is usually larger than that of the subatrial triactines, although this may not be of great importance. At first, we were inclined to consider the new species an extreme form of *S. hastifera*. However, we obtained partial 28S sequences of the two specimens (GenBank acc.nrs MF872774, MF872775, and MF872776) and in the phylogeny of Fig. 3 they did not group into the same clade with *Sycettusa hastifera* (GenBank acc.nrs MF872777 of RMNH Por. 9659, and MF872778 of ZMA Por. 13443) and *S. simplex* (Jenkin, 1908) (GenBank acc.nrs MF872779 of RMNH Por. 10154 and MF872781 of ZMA Por. 12446), supporting a separation at the species level. To investigate the molecular differences between *S. hastifera*, *S. hirsutissima* **sp.nov.** and *S. simplex*, we separately aligned and trimmed the available *Sycettusa* 28S sequences of these three species yielding a length of 403 sites. The sequences of *S. hirsutissima* **sp.nov.** were identical. They shared three site differences with *S. hastifera* and four with *S. simplex*. The latter two species differed only in a single site, despite being clearly distinct in habitus as *S. simplex* has an almost smooth surface (cf. below).

***Sycettusa simplex* (Jenkin, 1908)**

Figs 73a–e, 74a–f

Grantessa simplex Jenkin, 1908: 446, figs 93–97.

? *Leuconia wasinensis*; Burton 1959: 181 (not: Jenkin 1908)

Material examined. RMNH Por. 10154, Maldives, Faafu Atoll, Wallstreet, 3.119°N 72.979556°E, depth 12 m, scuba, coll. N.J. de Voogd, field nr. MAD10/MAS115, 20 February 2015; ZMA Por. 10338, Seychelles, Mahé, NE coast, Cap Maçons & Anse de Forbans, 4.7667°S 55.5167°E, reef, depth 0–6 m, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 612, 14 December 1992; ZMA Por. 12446, Seychelles, Amirantes, St. François Atoll, 7.0833°S 52.7333°E, reef, depth 0–10 m, snorkeling, coll. J.C. den Hartog, field nr. NIOP-E stat. 792(bis)/27, 4 January 1993.

Description. Light beige-colored groups of longer and/or shorter tubes (Fig. 73a), somewhat tangled, occasionally divided or with a side tube. Size of individual tubes up to 6 cm or more long, 0.5 cm wide. Surface uneven or slightly hispid. Oscules terminal, usually surrounded by a circle of diactines and/or trichoxeas. Beige color persists in alcohol (Figs. 73b–c). Consistency soft, slightly firm.

Aquiferous system. Syconoid.

Skeleton. (Figs. 73d–e) Inarticulate, with a cortical skeleton of regular or slightly sagittal triactines, subectosomal pseudodosagittal triactines, the long paired actines forming the choanosomal skeleton together with the

unpaired actines of subatrial sagittal triactines, and with an atrial skeleton of regular or slightly sagittal triactines smaller than those of the cortical skeleton. Diactines are present in the oscular region and also occur scattered in the choanosome supporting the inarticulated skeleton.

Spicules. (Figs 74a–f) Diactines, trichoxeas, cortical and atrial triactines, pseudosagittal triactines, sagittal triactines.

Diactines (Fig. 74a), fusiform, usually with one end lance-headed, variable in length, 210–701–1140 x 13–25.8–36 μm .

Trichoxeas (Fig. 74b), small, mostly broken, 120–182–235 x 2–2.4–3.5 μm .

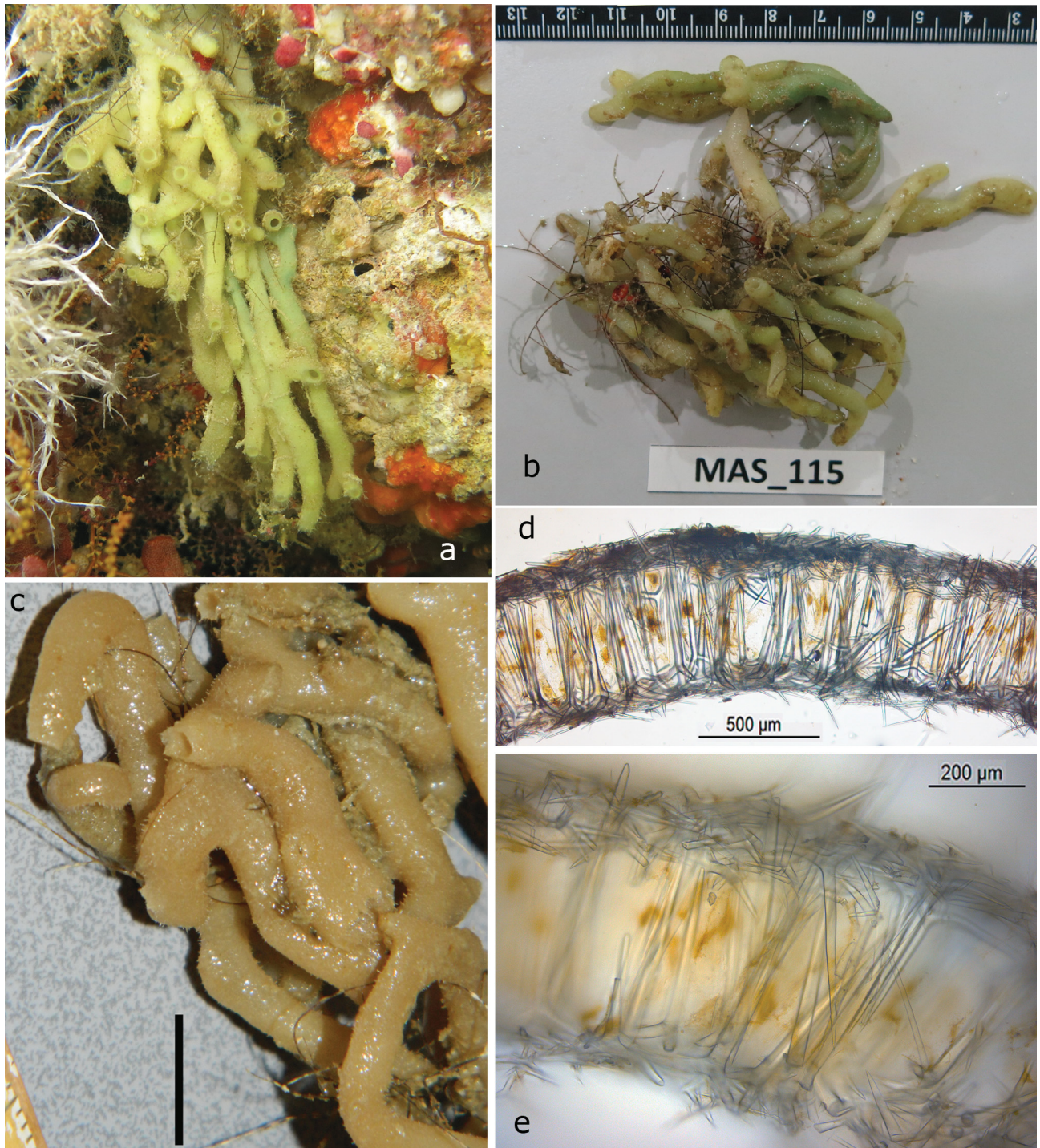


FIGURE 73. *Sycettusa simplex* (Jenkin, 1908), a–c, habitus of RMNH Por. 10154 from the Maldives, a, habitus in situ (photo N.J. de Voogd), b, on deck (photo N.J. de Voogd), c, preserved (scale bar = 1 cm), d, light microscopic image of cross section, e, detail of the same.

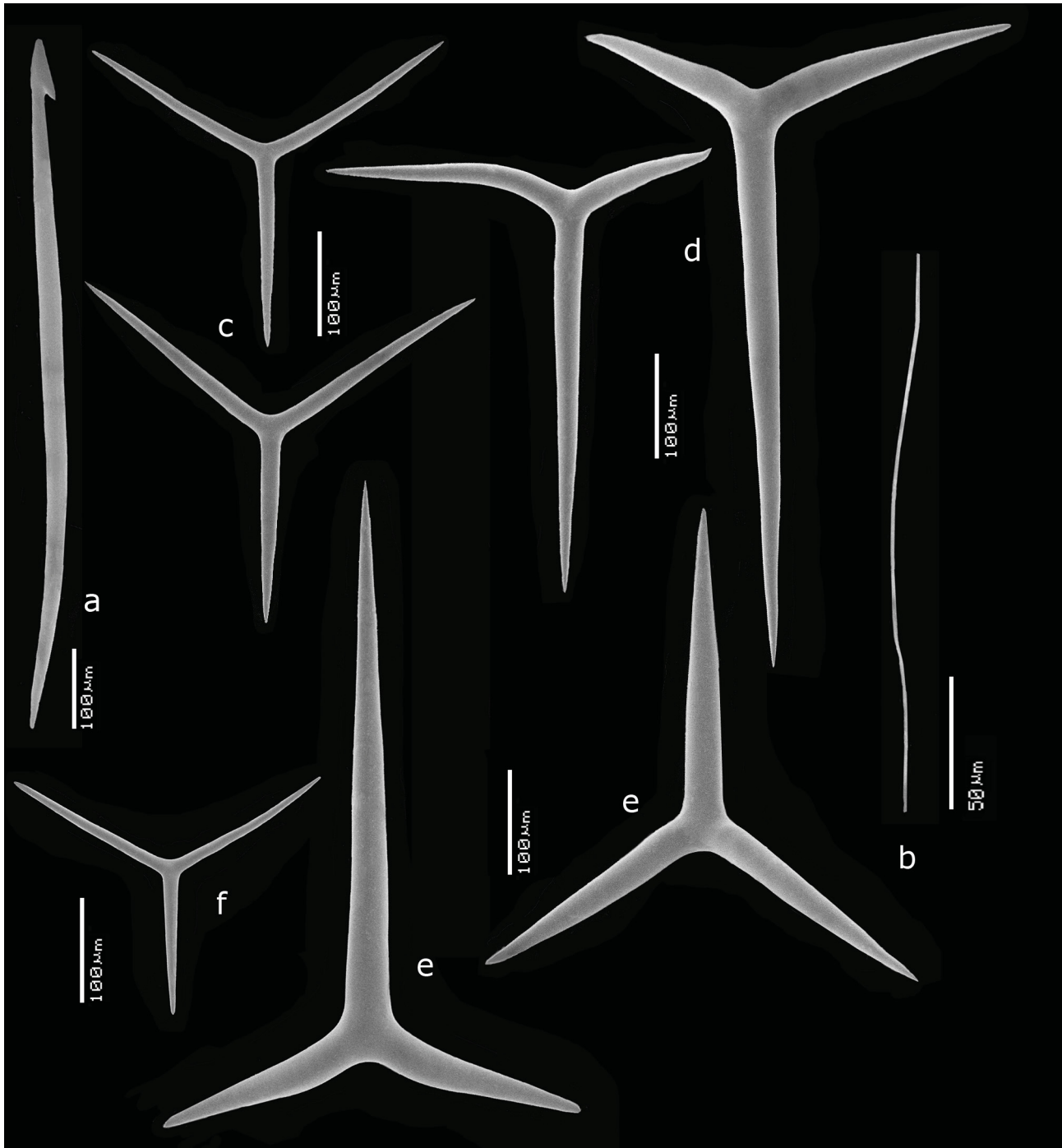


FIGURE 74. *Sycettusa simplex* (Jenkin, 1908), RMNH Por. 10154, from the Maldives, a–f, SEM images of the spicules, a, lance-headed giant diactine, b, broken trichoxea, c, cortical triactines, d, pseudosagittal triactines, e, sagittal subatrial triactines, f, atrial triactine.

Cortical triactines (Figs. 74c), variable in shape, from equiangular equireadate to sagittal or irregular, actines 183–219–288 x 12–17.4–24 µm.

Pseudosagittal triactines (Figs 74d), in a large size range, longest actines 241–369–504 x 18–21.4–30 µm, middle sized actines (usually the unpaired actine), 138–186–228 x 15–19.7–30 µm, shortest actines 64–132–241 x 14–18.9–26 µm.

Sagittal triactines (Figs 74e), variable in shape and in thickness, paired actines often almost forming T-shape, but occasionally more acutely angled, unpaired actines 396–436–538 x 17–29.6–44 µm, paired actines 179–232–282 x 19–26.7–39 µm.

Atrial triactines (Fig. 74f), regular, slightly sagittal or occasionally irregular, unpaired actine 114–142–181 x 10–11.4–14 µm, paired actines 101–154–201 x 9–10.4–12 µm.

Distribution and ecology. Maldives, Seychelles, Zanzibar, on reefs in shallow water.

Remarks. Jenkin's type material is closely similar both in shape and spicule sizes and shapes. Our identification with his species is made with confidence.

The three samples assigned here to *S. simplex* have similar spiculation as *S. stauridia* described below. The differences between the two species appear to be largely attributable to growth form, which is known to be a variable feature in many sponges. In contrast, 28S sequences of the two species were found to be substantially different (cf. Fig. 3). Molecularly, *S. simplex* is almost identical to *S. hastifera*, as we found only a single site difference in the above described inspection of a trimmed alignment of 403 sites, whereas differences between *S. simplex* and *S. stauridia* numbered 22 sites.

Voigt *et al.* (2012) sequenced a Seychelles specimen, ZMA Por. 11566 under the name *S. simplex*, but we reidentified this material as *S. zanzibarensis* (Jenkin, 1908) (see below).

Leucortis anguinea Ridley, 1884 from Providence in the Mascarene Islands is a *Sycettusa* according to Burton (1963). It has a shape reminding a bit of the present species, but the specimen is not likely the same as the present species judging from the description in Ridley 1884 (p. 629, pl. 53L, 54d), as it includes tetractines.

Sycettusa sibogae (Burton, 1930) as redescribed by Van Soest & De Voogd (2015) is similar to the present species, but has no giant diactines and its cortical triactines are twice as large.

We reexamined *Leuconia wasinensis* sensu Burton, 1959 from South Arabia (Murray Expedition station 45 nr. 537) kept in the Natural History Museum (BMNH 1936.3.4.537) and found this to be very similar to *Sycettusa simplex*. Its identity cannot be *Leucandrilla wasinensis* as it has a smooth tubular shape, not oval and hispid; it lacks an apical fringe and its skeleton is inarticulate. The subcortical triactines are pseudosagittal and both cortical and atrial skeleton consist of smaller triactines.

***Sycettusa stauridia* (Haeckel, 1872)**

Figs 75a–f, 76a–f

Djeddea violacea Miklucho-Maclay in Haeckel, 1872: 245 (*nomen nudum*).

Sycetta (*Sycettusa*) *stauridia* Haeckel, 1872: 236, 245, pl. 42 figs 13–16.

Grantessa stauridia; Lévi 1965: 26.

Material examined. ZMA Por. 02460, Eritrea, Dahlak Archipelago, Harmil Island, Red Sea, 16.5167°N 40.15°E, depth 1 m, scuba, coll. J.H. Stock, Israel South Red Sea Exped. 1962, field nr. E62-10418, 28 March 1962; ZMA Por. 13664, Israel. Gulf of Aqaba, containerport, on pillar, depth 5 m, scuba, coll. M. Wunsch, field nr. AQ68, 5 July 1998.

Description. Masses of small hollow lobes and tubes (Figs 75a–c). Surface faintly roughened, not smooth. Color in situ greyish blue to light red-brown, in alcohol both samples are red-brown. Size of whole mass up to 6 x 8 cm, individual tubes and lobes up to 1.5 cm high 1 cm in diameter or smaller. Oscules are frequently absent from the top of the hollow lobes, as they may be at the sides or in the interstices, and are not common. They do not have observable collars or fringe and have a diameter up to 0.5 cm.

Aquiferous system. Syconoid.

Skeleton. (Figs 75d–f) As usual, there is a cortical skeleton of triactines (Fig. 75e), an inarticulated choanosomal skeleton (Fig. 75d) formed by the longer paired actine of subectosomal triactines and the unpaired actines of subatrial triactines, and an atrial skeleton (Fig. 75f) of tangential triactines. Rare diactines and trichoxeas.

Spicules. (Figs 76a–f) Diactines, trichoxeas, cortical triactines, pseudosagittal triactines, large sagittal triactines, atrial triactines.

Diactines (Fig. 76a), fusiform, supporting the inarticulated skeleton in a low frequency, 269–426–541 x 15–16.6–19 µm.

Trichoxeas (Fig. 76b), rare, probably associated with the oscules, 200–650 x 2–6 µm.

Cortical triactines (Fig. 83c), almost regular equiangular equiradiate, 177–213–255 x 10–14.0–20 µm.

Pseudosagittal triactines (Figs 76d), longest actine 316–406–468 x 15–18.3–23 µm, middle sized actine 171–198–234 x 15–17.3–21 µm, shortest actine 108–168–201 x 15–16.9–20 µm.

Subatrial triactines (Fig. 76e), many are almost T-shaped, unpaired actines $328\text{--}423\text{--}510 \times 24\text{--}28.6\text{--}32 \mu\text{m}$, paired actines $241\text{--}272\text{--}336 \times 22\text{--}23.7\text{--}27 \mu\text{m}$.

Atrial triactines (Fig. 76f), more or less regular, actines $135\text{--}159\text{--}174 \times 8\text{--}11.1\text{--}13 \mu\text{m}$.

Distribution and ecology. Red Sea, in shallow water.

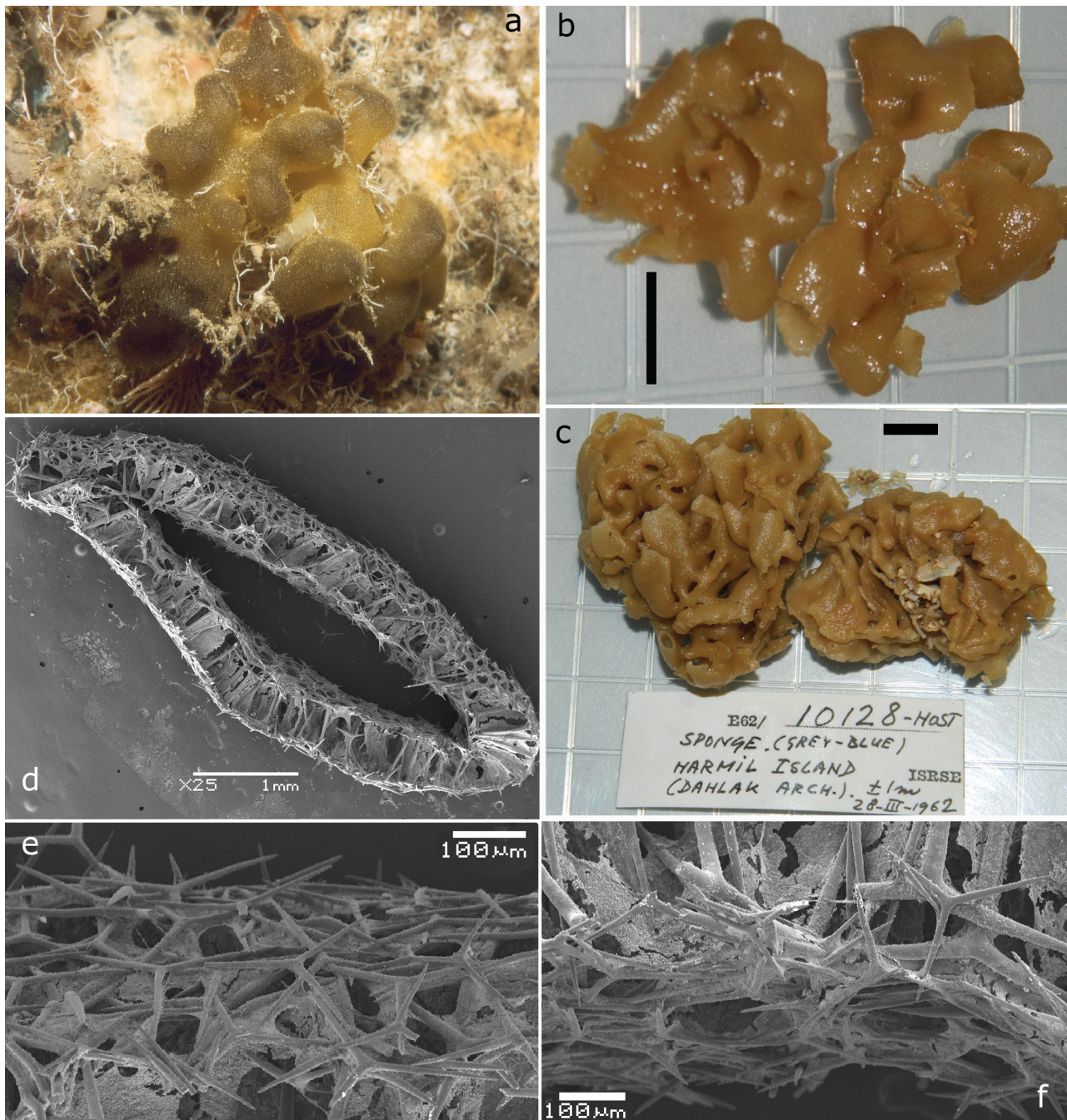


FIGURE 75. *Sycettusa stauridia* (Haeckel, 1872), from Red Sea localities, a–c, habitus in situ and preserved, a, ZMA Por. 13664, from Israel, Gulf of Aqaba, in situ on pillar of container port (photo M. Wunsch), b, the same preserved (scale bar = 1 cm), c, ZMA Por. 02460 from Eritrea, habitus preserved (scale bar = 1 cm) (specimen previously reported in Lévi, 1965), d–f, SEM images of sections of the skeleton of ZMA Por. 13664 from Gulf of Aqaba, d, cross section, e, cortical skeleton, f, atrial skeleton.

Remarks. We follow Lévi (1965) in assigning the specimens to Haeckel's *S. stauridia*, although his figure and description shows some discrepancies: Haeckel's specimen apparently was much smaller and he provided a stylized drawing which shows a single central tube with a ring of side tubes. He did not mention the presence of diactines. However, they are not very common in our specimens, so he may have overlooked them. He did not

make a distinction in pseudosagittal subcortical triactines and sagittal subatrial triactines. The sizes he provided of these spicules are similar to those of the present specimens, as are those of the other spicules.

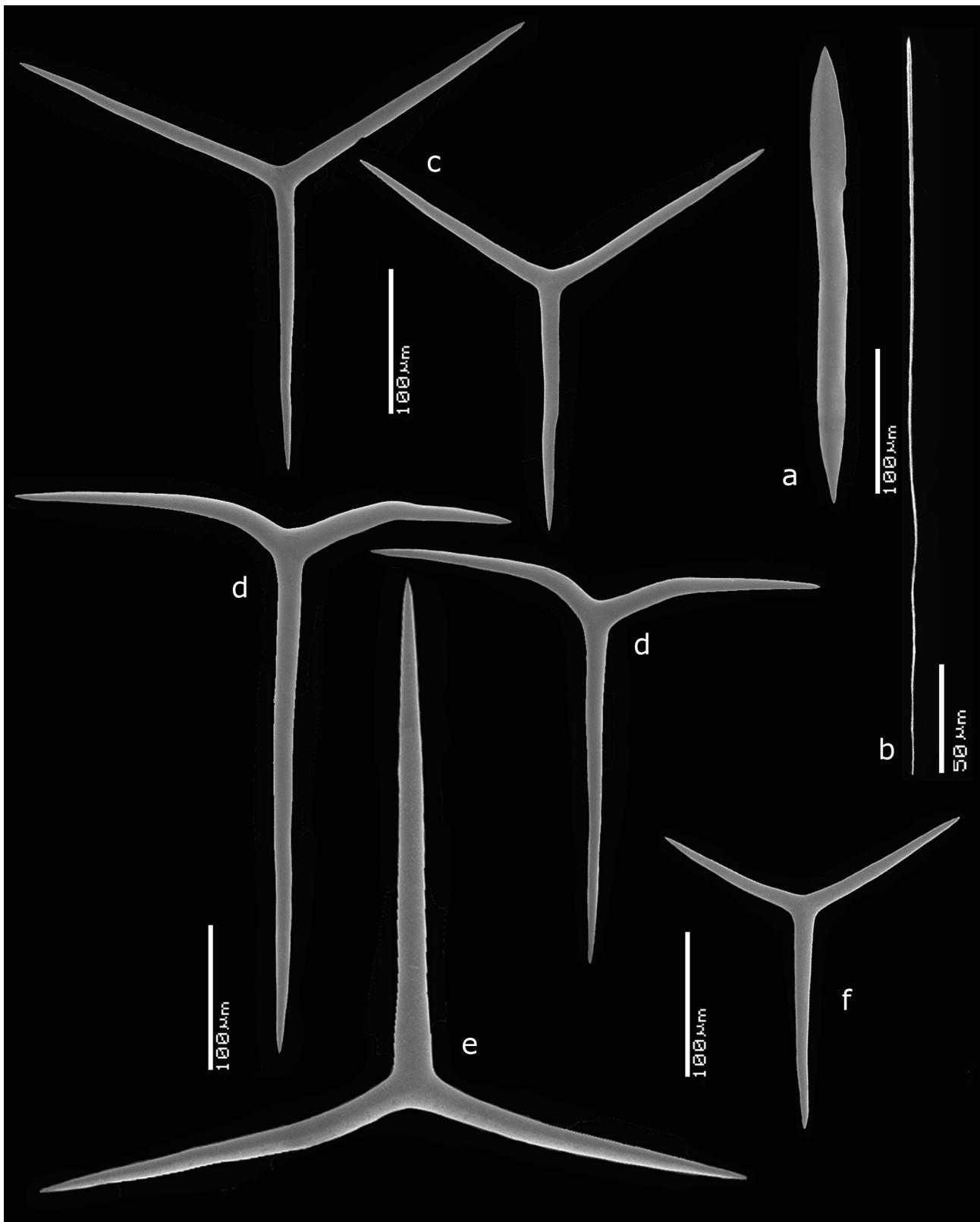


FIGURE 76. *Sycettusa stauridia* (Haeckel, 1872), ZMA Por. 02460, a–f, SEM images of the spicules, a, fusiform diactine, b, trichoxea, c, cortical triactines, d, pseudosagittal triactines, e, subatrial sagittal triactine, f, atrial triactine.

There are competing names, which are potential junior synonyms of this species. Mauritian *Sycortis sycilloides*

Schuffner, 1877 (p. 420, pl. 25 fig. 10) has similar habitus (two coalescent small tubular individuals), but it has the unpaired actines of the subatrial triactines much longer and thicker (600–1000 x 80 µm) against Haeckel's and ours only 400 x 10–20 µm. Red Sea *Grantessa glabra* Row, 1909 (p. 203, pl. 19 figs 5–6, text fig. 4a) is a small tube with side oscule and it has cortical and atrial triactines much larger (400–700 µm) and diactines and pseudosagittal triactines much thicker (50–90 µm) than Haeckel's and the present material. If these measurements would prove to be inaccurate or much more variable than so far determined, these names could be synonyms. Redescription is necessary. Burton (1959) reported *Grantessa glabra* from the South Arabian region and *Grantessa sycilloides* from the Gulf of Aden, but he did not provide a description of his material. He commented that the two species, *glabra* and *sycilloides*, are probably synonymous.

We obtained a 28S partial sequence of one of our specimens (ZMA Por. 13664). This ended up in the same clade but rather far away from the group comprised by *Sycettusa hastifera*-*S. simplex*-*S. hirsutissima* **sp.nov.** (cf. Fig.3). As mentioned above in the Remarks of *S. simplex*, a trimmed alignment with a length of 403 showed 20 sites or more difference with *S. hastifera*, *S. hirsutissima* and *S. simplex*.

***Sycettusa zanzibaris* (Jenkin, 1908)**

Figs 77a–g, 78a–i

Grantessa zanzibaris Jenkin, 1908: 448, figs 98–102; Burton 1959: 180.

Material examined. ZMA Por. 11491, Seychelles, Bird Island, off E coast, 3.7167°S 55.2167°E, reef, depth 3 m, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 717/08, 20 December 1992; ZMA Por. 11566, Seychelles, Amirantes, Île Desnoeufs platform, outer slope, 6.2167°S 53.0167°E, depth 12–15 m, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 738/22, 2 January 1993; ZMA Por. 11568, Seychelles, Amirantes, N of D'Arros Island, 5.4°S 53.3167°E, depth 45–55 m, on rhodolite bottom, dredge, coll. R.W.M. van Soest, field nr. NIOP-E stat. 752/13, 26 December 1992; ZMA Por. 12438, Seychelles, Amirantes, N of D'Arros Island, 5.4°S 53.3167°E, depth 45–55 m, on rhodolite bottom, dredge, coll. R.W.M. van Soest, field nr. NIOP-E stat. 752/11, 26 December 1992.

Description. Masses of short tubes (Figs 77a–b), beige-white to light brown in situ and on deck, pale transparent white in alcohol. The specimens have a quite characteristic glassy slippery appearance in alcohol. Size of largest mass up to 2 cm in lateral expansion, 1–2 cm high. Individual tubes up to 5 mm high, 3–4 mm in diameter, with the oscule about 1 mm diameter and surrounded by a thin collar. Consistency cartilaginous.

Aquiferous system. Syconoid.

Skeleton. (Figs 77c–g) Inarticulate (Figs 77c–d). The cortical skeleton (Fig. 77e) is a mixture of tangential triactines and short banana-shaped diactines, carried by the shortest paired actine and unpaired actine of subcortical pseudosagittal triactines. The inarticulate skeleton is made up of the longer actines of the subcortical pseudosagittal triactines and the unpaired actines of subatrial triactines. The atrial skeleton (Fig. 77f) consists of the paired actines of the subatrial triactines supported by two types of tetractines, smaller with all actines of almost similar length and thickness, and larger with enlarged apical actines protruding far into the atrial lumen. The small oscular collar (Fig. 77g) is formed by giant diactines, trichoxeas, triactines (similar to the subatrial triactines) and regular tetractines with a short apical actine.

Spicules. (Figs 78a–i) Diactines, trichoxeas, cortical triactines, pseudosagittal triactines, sagittal triactines, tetractines.

Giant diactines (Fig. 78a), fusiform 402–667–1100 x 12–20.6–29 µm.

Trichoxeas (Fig. 78b), invariably broken, fragments 240–330 x 2–3 µm.

Banana-shaped diactines (Fig. 78c), curved, asymmetrical, 141–162–204 x 7–8.1–9 µm.

Cortical triactines (Figs 78d), equiangular and equiradiate or more often with all actines of slightly different length or slightly sagittal, actines 84–103–126 x 6–8.3–10 µm.

Pseudosagittal triactines (Figs 78e), with middle actine straight or gently curved, and shortest actine with a characteristic angular curve, longest actines 81–146–183 x 6–6.9–8 µm, middle-sized actines 73–106–138 x 6–6.6–9 µm, shortest (unpaired) actines 59–88–111 x 6–6.8–8 µm.

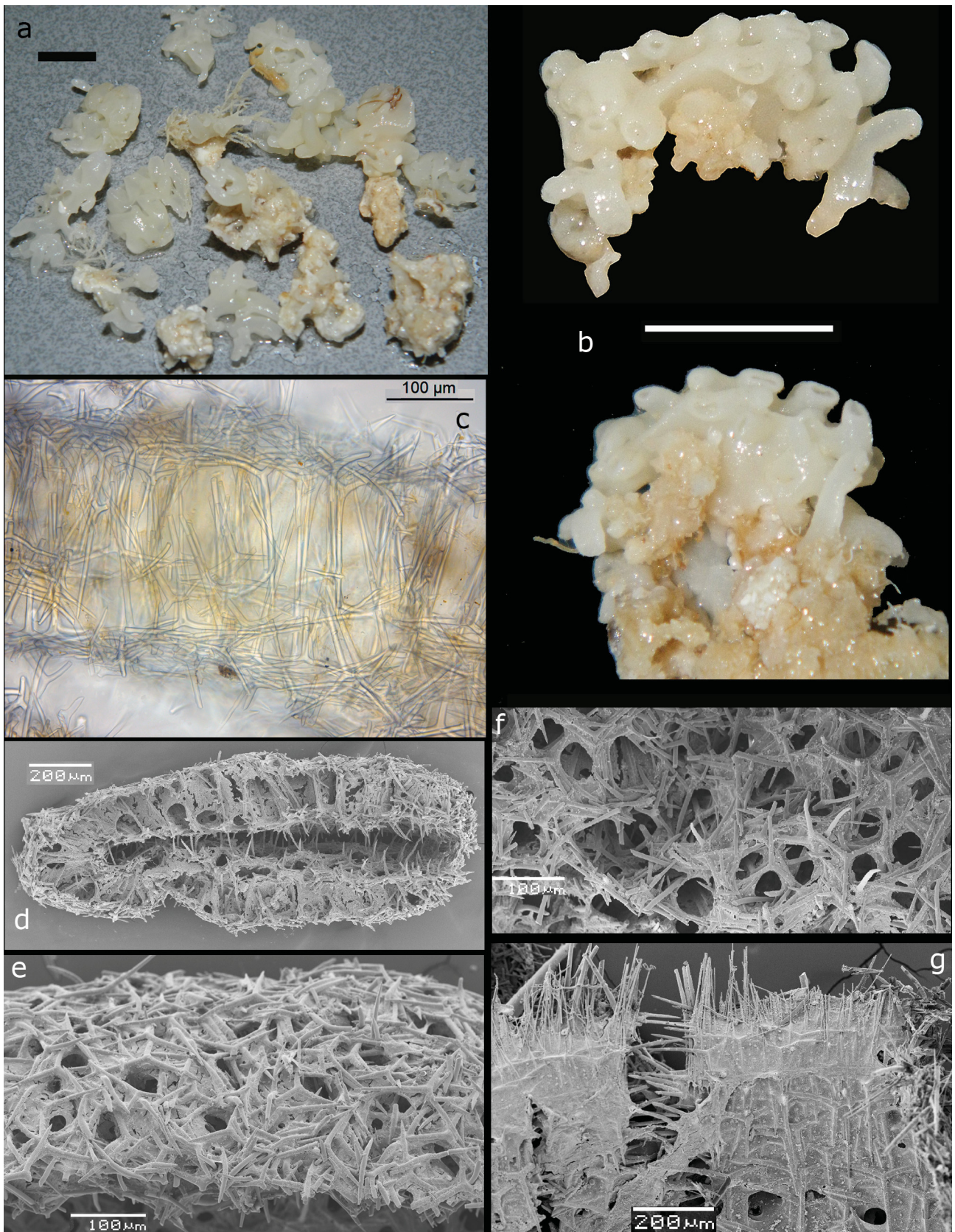


FIGURE 77. *Sycettusa zanzibaris* (Jenkin, 1908), a–b, habitus of preserved specimens from the Seychelles, a, ZMA Por. 11491 (scale bar = 1 cm), b, ZMA Por. 11566 (scale bar = 1 cm), c, light microscopic image of cross section of ZMA Por. 11566, d–g, ditto, SEM images of the skeleton, d, cross section, e, cortical skeleton, f, atrial skeleton, g, skeleton of the oscular rim.

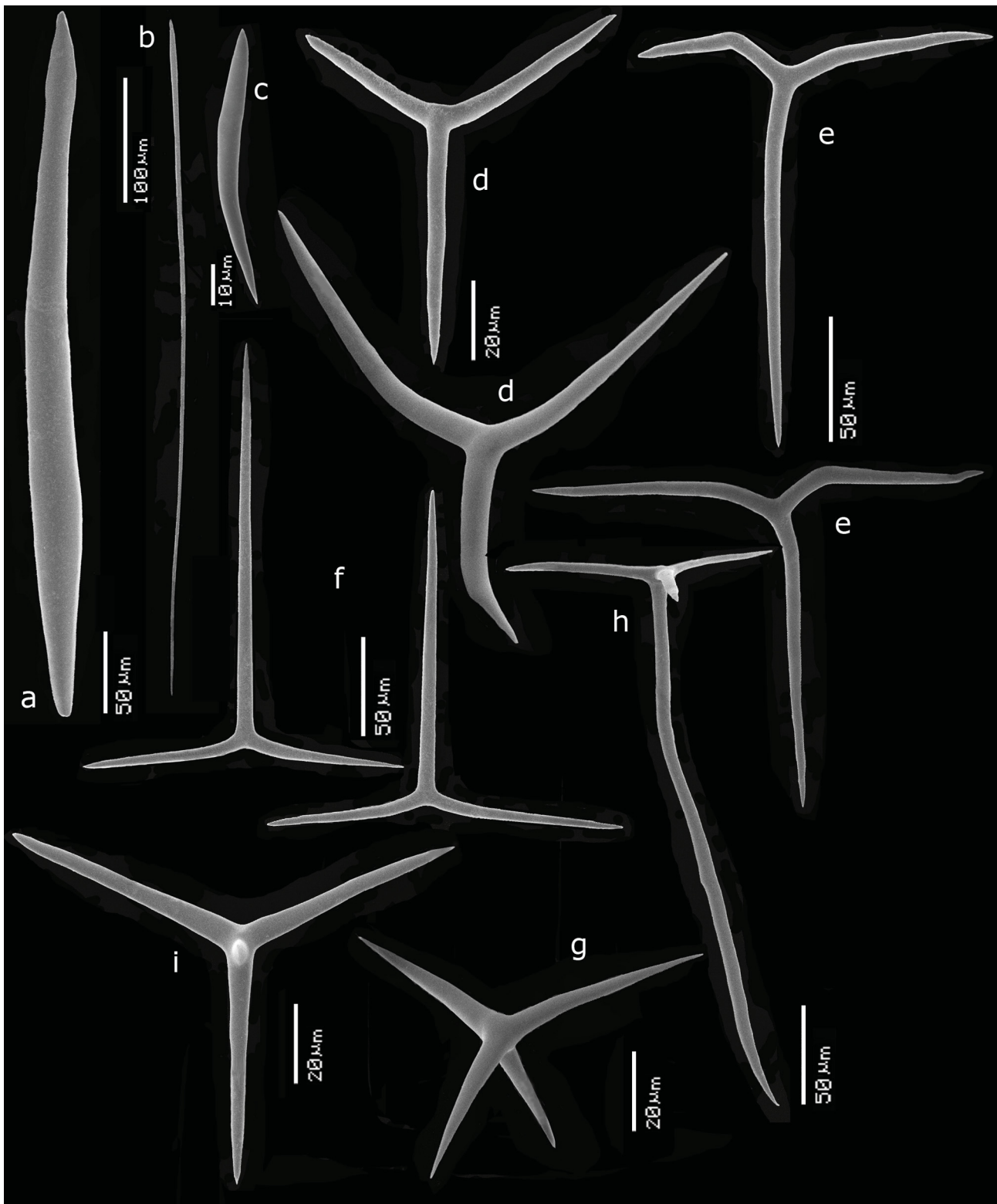


FIGURE 78. *Sycettusa zanzibaris* (Jenkin, 1908), ZMA Por. 11566, a–i, SEM images of the spicules, a, giant diactine, b, trichoxea, c, small cortical diactine, d, cortical triactines, e, pseudosagittal triactines, f, subatrial sagittal triactines, g, small atrial tetractine, h, atrial tetractine with long apical actine which protrudes into the atrial cavity, i, regular tetractine from the oscular rim.

Subatrial triactines (Figs 78f) (and triactines of the oscular collar), sagittal, almost T-shaped, unpaired actines 151–179–210 x 8–9.8–11 µm, paired actines 81–92–105 x 7–8.2–9 µm.

Small equiradiate tetractines (Fig. 78g), equiangular, but not equiradiate, with clear position of unpaired

actines, paired actines and curved apical actines; unpaired actines 54–69–84 x 5–6.3–8 µm, paired actines 76–97–111 x 6–6.7–7 µm, apical actines 37–56–84 x 5–5.7–7 µm.

Larger atrial tetractines (Fig. 78h), unpaired and paired actines similar in length, 62–95–112 x 5–6.6–8 µm, apical actines long, curved or sometimes slightly crooked, 105–229–432 x 6–7.1–9 µm.

Tetractines of the oscular collar (Fig. 78i), resembling subatrial sagittal triactines but with small curved apical actine; unpaired actines, 81–112–126 x 7–7.4–9 µm, paired actines 84–96–111 x 7–7.6–9 µm, apical actines 22–43–61 x 5–5.7–7 µm.

Distribution and ecology. Seychelles, Zanzibar, shallow water down to 55 m. Burton (1959) reported this species from the Southern Red Sea, but provided no description.

Remarks. The presence of tetractines and the characteristic angular curve of the unpaired actines of the pseudosagittal triactines distinguish this species from all other *Sycettusa* species of the Western Indian Ocean.

Voigt *et al.* (2012) used ZMA Por. 11566 for their study of the phylogeny of Calcarea (identified as *S. cf. simplex*). Voigt *et al.*'s sequence was compared with our own from ZMA Por. 11568 (see Fig. 74), and in an alignment trimmed to a length of 403 sites, we found two differences. Our partial 28S sequences of *Sycettusa zanzibaris* grouped in the same clade together with New Caledonian *S. tenuis* Borojević & Klautau, 2000 (downloaded from the Sponge Barcode Project site) away from mainstream *Sycettusa* species and closer to *Grantessa* species. *S. zanzibaris* and *S. tenuis* were found to exhibit 3 differences in the 403 sites alignment, so these are probably closely related. Borojević & Klautau 2000 (p. 198) stated in their remarks that *S. tenuis* was 'certainly close to *Sycettusa simplex* (Jenkin, 1908)', but as these authors admit, *S. simplex* has no tetractines (cf. Jenkin's description of the atrial skeleton and spicules on p. 449). Remarkably, they did not point out that *S. zanzibaris* rather than *S. simplex* is the closer species.

The position of the group of species comprising *Ute*, *Uteopsis* and *Grantessa* grouped in our phylogeny of Fig. 3 within the larger clade of *Sycettusa* species remains unclear for the moment.

Genus *Vosmaeropsis* Dendy, 1892

Vosmaeropsis glebula sp.nov.

Figs 79a–g

Material examined. Holotype, ZMA Por. 10608, Seychelles, La Digue Island, S coast, 4.3833°S 55.8333°E, depth 2 m, reef, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 735/28, 23 December 1992.

Paratypes, ZMA Por. 10553, Seychelles, Aride Island, S coast, 4.2167°S 55.6667°E, snorkeling, coll. J.C. den Hartog, field nr. NIOP-E stat. 711/12, 18 December 1992; ZMA Por. 10637, Seychelles, Amirantes, St. François Atoll, Île Bijoutier, depth 3 m, reef, scuba, coll. R.W.M. van Soest, field nr. NIOP-E stat. 792/20, 6 January 1993.

Description. Small lobes and short thick-walled tubes (Fig. 79a), occurring singly or in coalescent groups. The holotype consists of five such lobes, which were originally grouped together. Each lobe or tube carries a terminal oscule. Color in situ yellow-brown, in preservation they are similarly light brown. Size 1–2 cm in height, 0.5–1 cm in diameter, oscules about 2 mm in diameter, flush, without rim or fringe. Consistency soft.

Aquiferous system. Leuconoid.

Skeleton. (Figs 79b–c) In our SEM cross section (Fig. 79b), which is admittedly rather confused, from surface to atrium there is a cortical skeleton of smaller sagittal and larger regular triactines (Fig. 79c), supported by subcortical pseudosagittal triactines replaced by giant triactines in the main skeleton. In the atrial region there are larger triactines rather similar to the cortical triactines but supported by smaller, more or less regular triactines.

Spicules. (Figs 79d–h) Triactines only, tentatively divisible into cortical triactines, giant triactines, pseudosagittal triactines, subatrial triactines and atrial triactines.

Cortical triactines (Fig. 79d), regular, usually with straight actines, intermediate in size, actines 76–168–258 x 8–15.1–31 µm.

Pseudosagittal triactines (Fig. 79f), longest actines 270–474–662 x 18–36.7–47 µm, middle sized actines 167–261–330 x 17–32.1–40 µm, shortest (=unpaired) actines 81–129–292 x 18–32.8–41 µm.

Giant or large triactines (Fig. 79e) of the main skeleton, tending to be more or less equiangular and equiradiate, 302–567–779 x 32–57.4–78 µm.

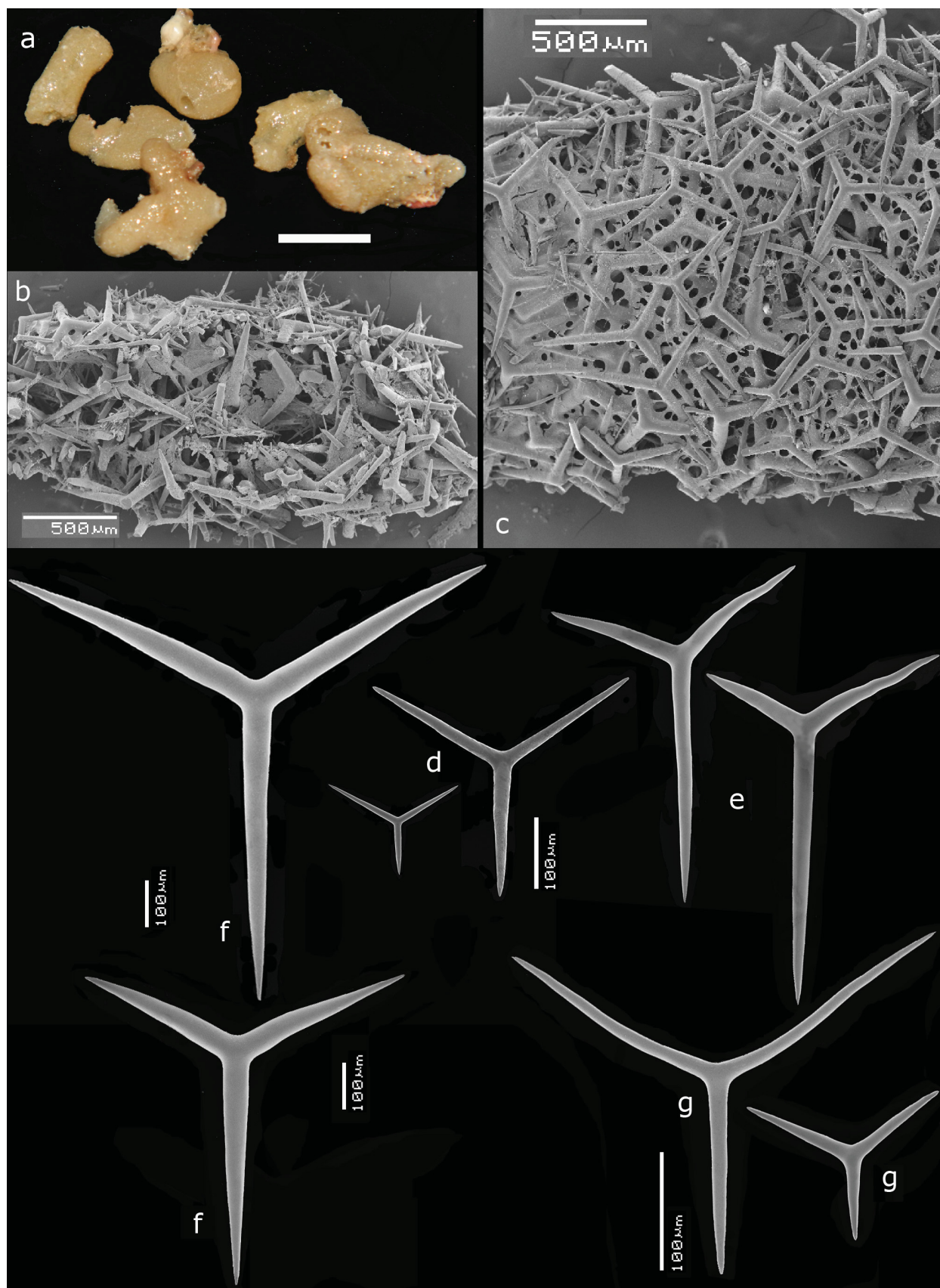


FIGURE 79. *Vosmaeropsis glebula* **sp.nov.**, holotype ZMA Por. 10608 from the Seychelles, a, preserved habitus (scale bar = 1 cm), b–c, SEM images of skeleton, b, cross section through the wall, c, view of the surface skeleton, d–g, SEM images of the spicules, d, cortical sagittal triactine, e, subcortical pseudosagittal triactines, f, giant and large choanosomal triactines, g, subatrial and atrial triactines.

Subatrial and atrial triactines (Figs 79g), slightly sagittal, intermediate and smaller triactines, often with incurved paired actines; unpaired actines 93–141–233 x 15–20.3–26 µm, paired actines 111–195–271 x 15–19.6–24 µm.

Distribution and ecology. Known only from several localities in the Seychelles, reefs, shallow water.

Etymology. Glebula (L.) meaning small lump, referring to the habitus.

Remarks. The new species is assigned to *Vosmaeropsis* on account of the confused choanosomal skeleton in combination with pseudosagittal triactines. So far, no *Vosmaeropsis* species are known from the Western Indian Ocean (cf. Cavalcanti *et al.* 2015; Van Soest *et al.* 2018). The new species differs from most Indo-West Pacific *Vosmaeropsis* species, including e.g. *V. grisea* Tanita, 1939 as described by us from Indonesia (cf. Van Soest & De Voogd 2015), in the lack of (giant) diactines and tetractines. Only two species in that wide area share the lack of diactines and tetractines with our new species. In Philippine deeper water occurs *V. connexiva* (Poléjaeff, 1883), which differs from our specimens in the apparent lack of small cortical and atrial triactines, while the pseudosagittal triactines are smaller than those of the new species, with longest actines not exceeding 400 x 20–25 µm (in our specimens up to 662 x 47 µm). The habit of the species is not clear as Poléjaeff only had a few fragments. New Caledonian *V. hozawai* Borojević & Klautau, 2000 is a larger (5 cm) dark brown, sac-shaped sponge from 20–25 m depth. It differs especially in the much larger size of the giant triactines, which are up to 1500 x 100 µm (ours 779 x 78 µm); likewise the regular cortical and atrial triactines are larger, up to 420 x 17 µm (ours up to 271 x 26 µm). Despite the lack of illustrations for these two species, the differences are here considered sufficiently great to judge them to be different from our new species. In the area considered here there are no reports of additional *Vosmaeropsis* species.

Unfortunately, our attempt to obtain a partial 28S sequence of the type material failed.

Family Amphoriscidae Dendy, 1893

Genus *Amphoriscus* Haeckel, 1872

Amphoriscus semoni Breitfuss, 1896

Figs 80a–e, 81a–d

Amphoriscus semoni Breitfuss, 1896: 435; Breitfuss 1898: 221; Van Soest & De Voogd 2015: 93, figs 68a–f.

Material examined. ZMA Por. 10527, Seychelles, NE of Aride Island, 4.1667°S 55.7333°E, depth 55 m, Agassiz trawl, coll. R.W.M. van Soest, field nr. NIOP-E stat. 714/01, 19 December 1992.

Description. The sample consists of a dozen small thin tubes (Fig. 80a), which are mostly loose, but two tubes are attached together to a small stone. It is likely the tubes were in contact on the substratum. Live color reported as white, in alcohol they become beige. Size of individual tubes 1–3 cm high, 5–9 mm in diameter. Apical oscules naked. Consistency soft.

Aquiferous system. Syconoid.

Skeleton. (Figs 80b–e) Inarticulate (Fig. 80b). The cortical skeleton (Figs 80c–d) is formed by the unpaired and paired actines of giant tetractines. The apical actines of the ectosomal tetractines form the choanosomal skeleton together with the unpaired actines of subatrial sagittal triactines. The subatrial skeleton is formed by the paired actines of sagittal triactines and all actines of smaller triactines. The atrial skeleton (Fig. 80e) is formed by small tetractines, the apical actines of which protrude into the atrial lumen.

Spicules. (Figs 81a–d) Giant tetractines, triactines, small tetractines.

Giant tetractines (Fig. 81a), with straight or curved actines of rather variable length and thickness, unpaired actines 162–264–487 x 12–20.1–31 µm, paired actines 210–336–552 x 12–21.1–29 µm, apical actines 239–425–882 x 13–21.8–31 µm.

Triactines (Figs 81b–c), divisible in overlapping larger and smaller spicules:

Large triactines (Fig. 81b), sagittal, usually with unpaired actines slightly shorter; unpaired actines 200–266–342 x 13–14.8–18 µm, paired actines 279–309–336 ≈ 12–13.3–15 µm.

Small triactines (Fig. 81c), slightly sagittal, unpaired actines 48–137–180 x 7–9.4–14 µm, paired actines 88–178–246 x 6–8.8–11 µm.

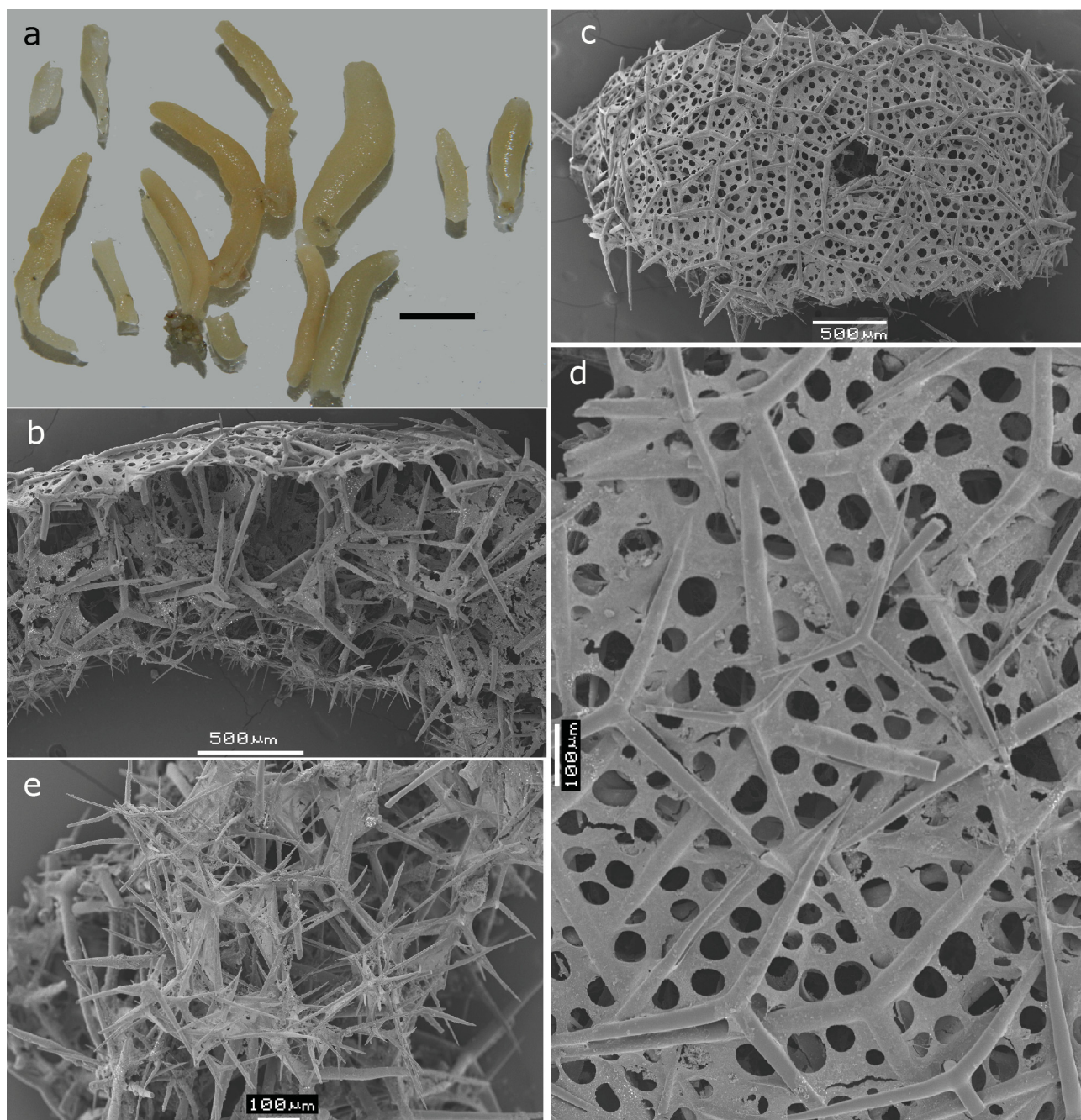


FIGURE 80. *Amphoriscus semoni* Breitfuss, 1896, ZMA Por. 10527 from the Seychelles, a, habitus of group of individuals (scale bar = 1 cm), b–e, SEM images of skeleton, b, cross section of body wall, c, overview from above of peripheral skeleton, d, detail of peripheral skeleton, e, overview from above of atrial skeleton.

Small tetractines (Figs 81d), sagittal, often with curved or wobbly paired actines; unpaired actines $81\text{--}150\text{--}241 \times 7\text{--}9.4\text{--}11 \mu\text{m}$, paired actines $121\text{--}214\text{--}269 \times 7\text{--}9.8\text{--}12 \mu\text{m}$, apical actines $15\text{--}54\text{--}94 \times 3\text{--}5.2\text{--}7 \mu\text{m}$.

Distribution and ecology. Indonesia, Seychelles, shallow-water down to 55 m.

Remarks. We assign this material to the Indonesian species *A. semoni* because of overall similarity with recently described material (cf. Van Soest & De Voogd 2015). However, there are several discrepancies: the tubes of the Indonesian ZMA Por. 08073 were described as green in life, and they also appeared slightly different in shape as their diameter gradually narrowed down towards the substratum, whereas our present specimens were white in life and remain cylindrical over most of their length. The apical actines of the giant tetractines of the Indonesian specimens penetrated through the atrial wall, which we do not observe in the present specimens. We consider these differences as minor and subject to variation.

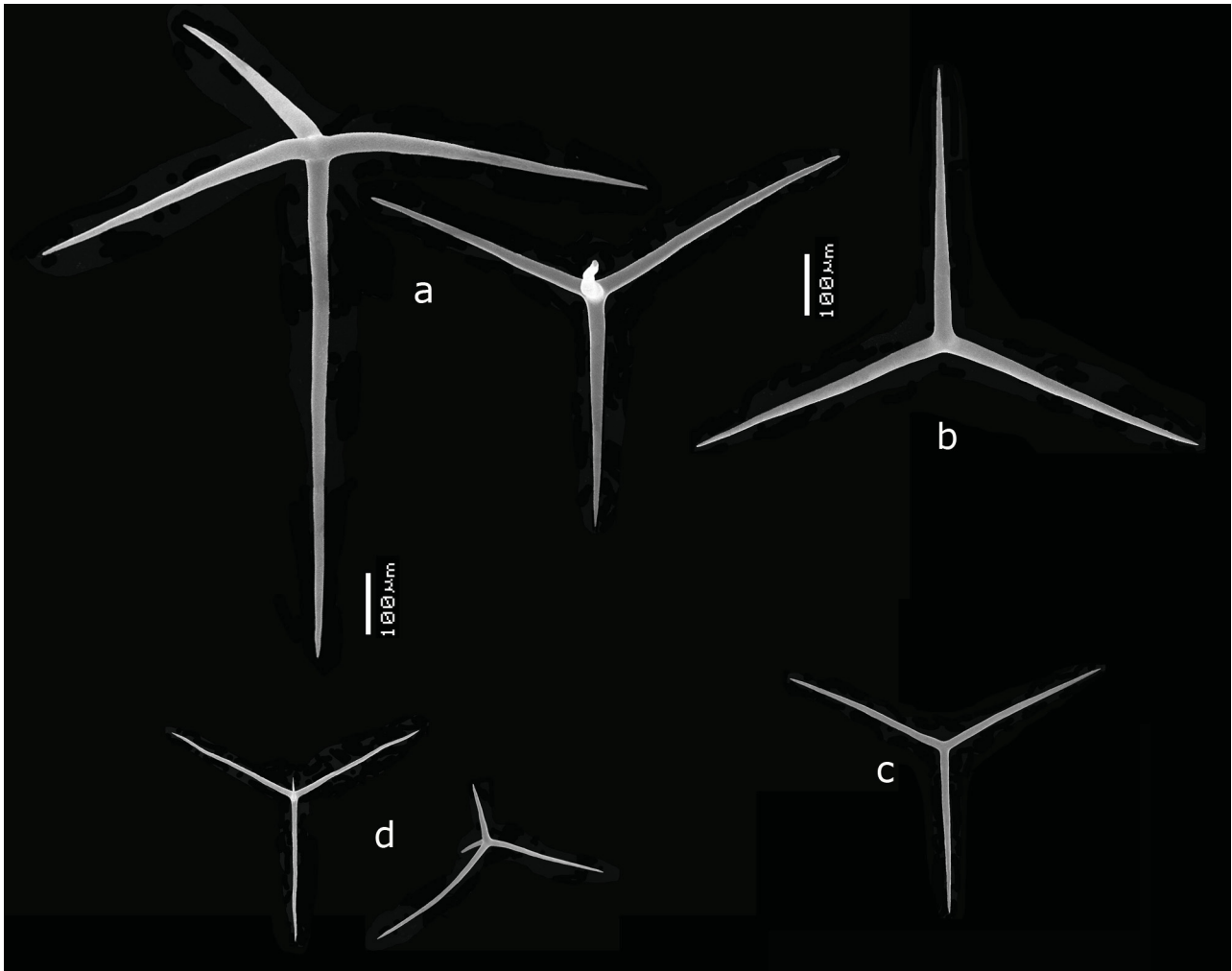


FIGURE 81. *Amphoriscus semoni* Breitfuss, 1896, ZMA Por. 10527, SEM images of the spicules, a, giant tetractines, b, giant triactine, c, subatrial triactine, d, atrial tetractines.

The South African *Amphoriscus kryptoraphis* Urban, 1908, from deeper water (155 m) differs from the above a.o. by the possession of trichoxeas.

Unfortunately, our attempt to obtain partial 28S sequences failed.

Genus *Paraleucilla* Dendy, 1892

Paraleucilla crosslandi (Row, 1909)

Figs 82a–h

Leucilla crosslandi Row, 1909: 207, fig. 6.

Leucandra innominata Dendy & Row, 1913: 774.

Paraleucilla crosslandi; Borojević *et al.* 2002: 1180.

Material examined. ZMA Por. 13439. Israel, Gulf of Aqaba, Red Sea, depth 7 m, scuba, coll. M. Wunsch, field nr. AQ7, 30 June 1998.

Description. Fragment of a short, squat, tube (Fig. 82a), white in life and in alcohol. Size 9 mm high, 6 mm in diameter, terminal oscule 3 mm. Consistency firm.

Aquiferous system. Leuconoid.

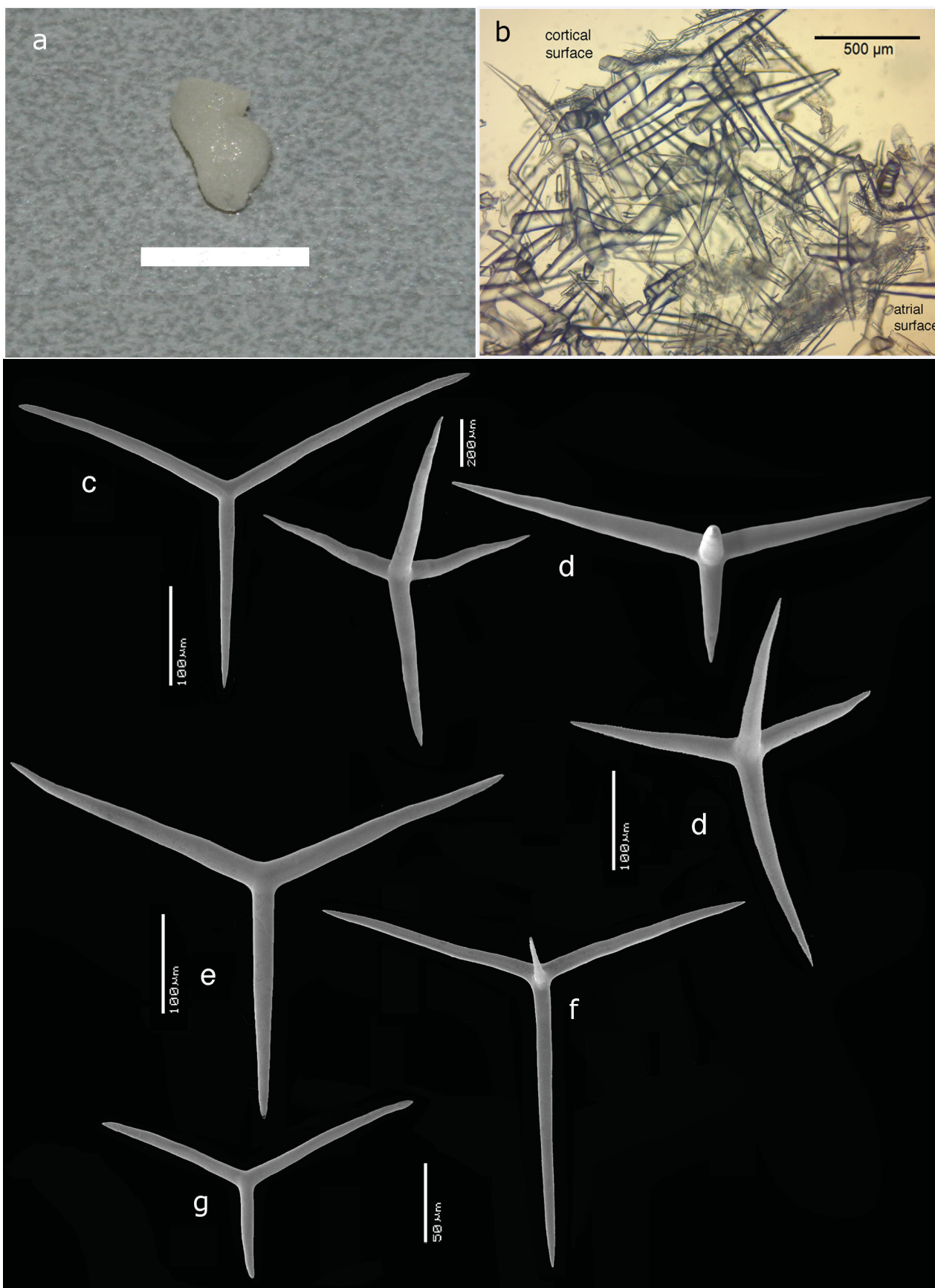


FIGURE 82. *Paraleucilla crosslandi* (Row, 1909), ZMA Por. 13439, from Gulf of Aqaba, a, habitus (scale bar = 1 cm), b, light microscopic images of cross section of skeleton, c–g, SEM images of the spicules, c, cortical triactine, d, (sub)cortical tetractines, e, large choanosomal triactines, f, large subatrial tetractines, g, atrial triactines.

Skeleton. (Fig 82b) In cross section of the wall there is a cortical skeleton of triactines and the unpaired and paired actines of cortical tetractines. The subcortical skeleton is inarticulate consisting of the apical actines of the cortical tetractines and the unpaired actines of ‘subatrial’ tetractines, which have a position in the middle of the wall. The mid-skeletal and subatrial region contains a confused mass of smaller tetractines, carried by a layer of smaller triactines lining the atrial cavity.

Spicules. (Figs 82c–h) Cortical triactines, giant tetractines, choanosomal triactines, subatrial tetractines, atrial triactines.

Large triactines, cortical (Fig. 82c) and mid-skeleton (Fig. 89e), which are indistinguishable morphologically; regular or slightly sagittal, actines $198\text{--}273\text{--}336 \times 10\text{--}17.9\text{--}27 \mu\text{m}$.

Giant tetractines (Fig. 82d), cortical, and mid-skeleton tetractines (these are not easily distinguishable morphologically), sagittal to irregular, often with arched paired actines and opposing unpaired and apical actines; unpaired actines $204\text{--}481\text{--}720 \times 23\text{--}76.7\text{--}98 \mu\text{m}$, paired actines $540\text{--}722\text{--}920 \times 21\text{--}56.3\text{--}88 \mu\text{m}$, apical actines $233\text{--}718\text{--}1030 \times 39\text{--}70.1\text{--}78 \mu\text{m}$.

Small tetractines of the subatrial skeleton (Fig. 82f), sagittal, unpaired actines $80\text{--}155\text{--}211 \times 8\text{--}10.2\text{--}11 \mu\text{m}$, paired actines $120\text{--}191\text{--}282 \times 8\text{--}10.4\text{--}11 \mu\text{m}$, apical actines $24\text{--}35\text{--}48 \times 7\text{--}8.2\text{--}9 \mu\text{m}$.

Small triactines of the atrial skeleton (Fig. 82g), $63\text{--}118\text{--}200 \times 8\text{--}10.3\text{--}14 \mu\text{m}$.

Distribution and ecology. Red Sea, shallow depth.

Remarks. The present specimen conforms closely with Row’s description. However, descriptions by Haeckel (1872, p. 156–157), of *Leucaltis bathybia* var. *perimina* (from a depth of 615 m) and *L. b.* var. *arabica* (shallow depth) from the Red Sea remind of the present species. Various authors assigned these names to different genera: *Leucaltis*, *Leuconia*, *Leucilla* and *Sycettusa*. There are insufficient details in Haeckel’s descriptions to decide whether *Leucaltis bathybia* is a senior synonym of *Paraleucilla crosslandi*. Burton (1952) reported *L. bathybia* (as *Leuconia*) from the Gulf of Aqaba giving measurements of the giant tetractines only, ranging from $400\text{--}960 \times 32\text{--}90 \mu\text{m}$. Given these large sizes it is possible that Burton’s specimens conform to *P. crosslandi*, but in the absence of further spicule measurements this cannot be ascertained. Remarkably, Burton did not discuss Row’s species. Unfortunately, also Lévi (1965) when reporting this species (as *Leuconia bathybia*) failed to give a description.

Dendy & Row’s (1913) new name *Leucandra innominata*, erected to remove the junior secondary homonymy of Row’s *Leucilla crosslandi* with Thacker’s (1908) *Leucandra crosslandi*, is no longer necessary because the homonymy of the two species names involved has been removed as they are reassigned to different genera. Because the replacement name *Leucandra innominata* was only used once in Burton’s (1963: 546) listing under the alleged senior synonym *Amphoriscus saccharata* (along with *Leucilla crosslandi*), which does not count as ‘use’ in the sense of ICZN art. 59.3, the name *Paraleucilla crosslandi* (Row, 1909) is reinstated.

Unfortunately, we were unable to obtain a partial 28S sequence for this species.

***Paraleucilla erpenbecki* sp.nov.**

Figs 83a–d, 84a–i

Material examined. Holotype, ZMA Por. 22409a, Mozambique Channel, between Mozambique and Madagascar, E of Juan de Nova Island, $17.2817^{\circ}\text{S } 43.1567^{\circ}\text{E}$, depth 60 m, coll. RV ‘Pelagia’ Around Africa II expedition, leg 6, field nr. 20-ASC10, 1 April 2001

Paratypes, ZMA Por. 22409c, five individuals from the same locality as the holotype.

Description. The sample consists of six sycon-like tubular individuals (Figs 83a,a1), one of which was chosen as the holotype (Fig. 83a). Shape oval, narrowing towards the osculum. Height of largest tube (the holotype) is 3 cm, diameter 1.5 cm. Fringe prominent but short, 2–3 mm, slightly flaring. Color in alcohol light beige. Surface slightly hispid, rough-looking. Consistency soft.

Aquiferous system. Leuconoid.

Skeleton. (Figs 83b–d) The wall has a thickness of about 2 mm with protruding trichoxeas and very few diactines causing the hispid surface. In the SEM cross section (Fig. 83b), from the periphery towards the atrium, there is a cortical skeleton (Fig. 83c) of rare triactines carried by the basal actines of a single layer of cortical tetractines. Occasionally, there are scattered diactines protruding from the skeleton to the outside. Next, the

choanosomal skeleton is inarticulate (Fig. 83b) formed by the apical actines of the cortical tetractines and unpaired actines of giant triactines lying in the mid-region of the wall. Below these there is a confused mass of smaller tetractines and triactines, and finally the atrial skeleton (Fig. 83d) is formed by tetractines of which the apical actines protrude far into the atrial lumen, and by smaller triactines. The fringe is formed by thin giant diactines grading into thick trichoxeas, and at the base it is supported by triactines and tetractines (not shown).

Spicules. (Figs 84a–i) Giant diactines, trichoxeas, small diactines, large tetractines, large triactines, small tetractines and small triactines.

Giant diactines (Fig. 84a), fusiform, blunt endings, $388\text{--}1066\text{--}1973 \times 19\text{--}31.8\text{--}42 \mu\text{m}$.

Trichoxeas and thin diactines (Fig. 84b), sharp endings but subapically often slightly distended, almost invariably broken, fragments measuring $480\text{--}962\text{--}1740 \times 3\text{--}4.8\text{--}7 \mu\text{m}$.

Small diactines (Fig. 84c), not common, only a few could be measured, $147\text{--}210 \times 8\text{--}9 \mu\text{m}$.

Cortical triactines and small triactines of the subatrial region (Figs 84d), these were indistinguishable and not very common, either regular or slightly irregular or sagittal, actines $138\text{--}196\text{--}266 \times 8\text{--}10.9\text{--}16 \mu\text{m}$.

Cortical large tetractines (Fig. 84e), not very common, with basal actines often curved and blunt ending, apical actines straight and pointed, thinner than the other actines; unpaired actines $132\text{--}324\text{--}468 \times 13\text{--}30.5\text{--}37 \mu\text{m}$, paired actines $216\text{--}304\text{--}429 \times 15\text{--}21.7\text{--}31 \mu\text{m}$, apical actines $211\text{--}321\text{--}786 \times 18\text{--}17.1\text{--}23 \mu\text{m}$.

Giant triactines (Figs 84f), sagittal with straight unpaired actines and curved paired actines; unpaired actines $151\text{--}320\text{--}603 \times 10\text{--}20.4\text{--}33 \mu\text{m}$, paired actines $231\text{--}366\text{--}598 \times 12\text{--}22.2\text{--}36 \mu\text{m}$.

Giant tetractines of the subatrial region (Fig. 84g), with straight actines, apical actines short and conical; unpaired actines $231\text{--}394\text{--}696 \times 13\text{--}18.8\text{--}38 \mu\text{m}$, paired actines $228\text{--}313\text{--}391 \times 12\text{--}16.7\text{--}26 \mu\text{m}$, apical actines $45\text{--}62\text{--}84 \times 7\text{--}8.3\text{--}10 \mu\text{m}$.

Small tetractines of the subatrial region (Fig. 84h), similar in shape to giant tetractines, but smaller, unpaired actines $48\text{--}149\text{--}268 \times 7\text{--}10.4\text{--}13 \mu\text{m}$, paired actines $63\text{--}151\text{--}249 \times 6\text{--}9.0\text{--}11 \mu\text{m}$, apical actines $31\text{--}47\text{--}61 \times 5\text{--}7.2\text{--}10 \mu\text{m}$.

Atrial tetractines (Fig. 84i), with long straight apical actines and unpaired actines almost similar in length, with curved paired actines; unpaired actines $152\text{--}232\text{--}418 \times 9\text{--}11.3\text{--}13 \mu\text{m}$, paired actines $174\text{--}285\text{--}461 \times 8\text{--}9.1\text{--}12 \mu\text{m}$, apical actines $66\text{--}167\text{--}234 \times 8\text{--}8.9\text{--}10 \mu\text{m}$.

Distribution and ecology. Mozambique Channel, at 60 m depth.

Etymology. Named after Dr. Dirk Erpenbeck, München, Germany, in recognition of his great efforts to integrate molecules and morphology in the classification of the Porifera.

Remarks. The new species is assigned to *Paraleucilla* on account of the skeletal zonation of an inarticulate subcortical skeleton formed by the apical actines of the cortical tetractines and the unpaired actines of giant triactines in the mid region of the choanosome, followed by a confused choanosomal and subatrial skeleton.

A regional species is *Paraleucilla proteus* (Dendy, 1913) (originally as *Leucilla*). It has the same shape (although much smaller: only 7 mm high) as our new species. Differences are that almost all spicules, excepting the subcortical tetractines, are considerably smaller in size, notably the giant triactines do not seem to be represented, the apical actines of the atrial tetractines are much shorter, and there are no giant diactines (though smaller diactines are present). There are also no cortical small triactines. Dendy suggested that his small specimens were juveniles of the Australian species *Leucilla australiensis* (Carter, 1886), but eventually Borojević *et al.* (2000) assigned Dendy's species to *Paraleucilla*.

A further geographically close species is *Paraleucilla cucumis* (Haeckel, 1872) (p. 205, as *Leucandra*) from Sri Lanka and South Australia, differing a.o. in the presence of subcortical and mid-region tetractines (the latter not present in our new species), and the absence of mid-region and atrial triactines, with as a consequence the absence of apical actines protruding into the atrial lumen. There is a small nomenclatorial problem, because Haeckel (1872) divided his *Leucandra cucumis* into two (?) varieties ('spezifische Varietäten'), *L.c.* var. *bassensis* and *L.c.* var. *palcensis*. The difference was the virtual absence (*bassensis*) and presence (*palcensis*) of giant diactines. The difference was apparently considered trivial because neither Dendy (1892) and Dendy & Row (1913), nor Cavalcanti *et al.* (2014) make mention of these varieties. We formally need to indicate which one of the varieties is the nominotypical variety (ICZN art. 47). In view of the redescription by Dendy (1892) it makes sense to consider the var. *bassensis* as the typical variety, to be named *Leucandra cucumis* var. *cucumis*, with the var. *palcensis* as a junior synonym. The latter name would then be available if future research would result in distinction of an Indian Ocean species differing from the Bass Strait *Paraleucilla cucumis*.

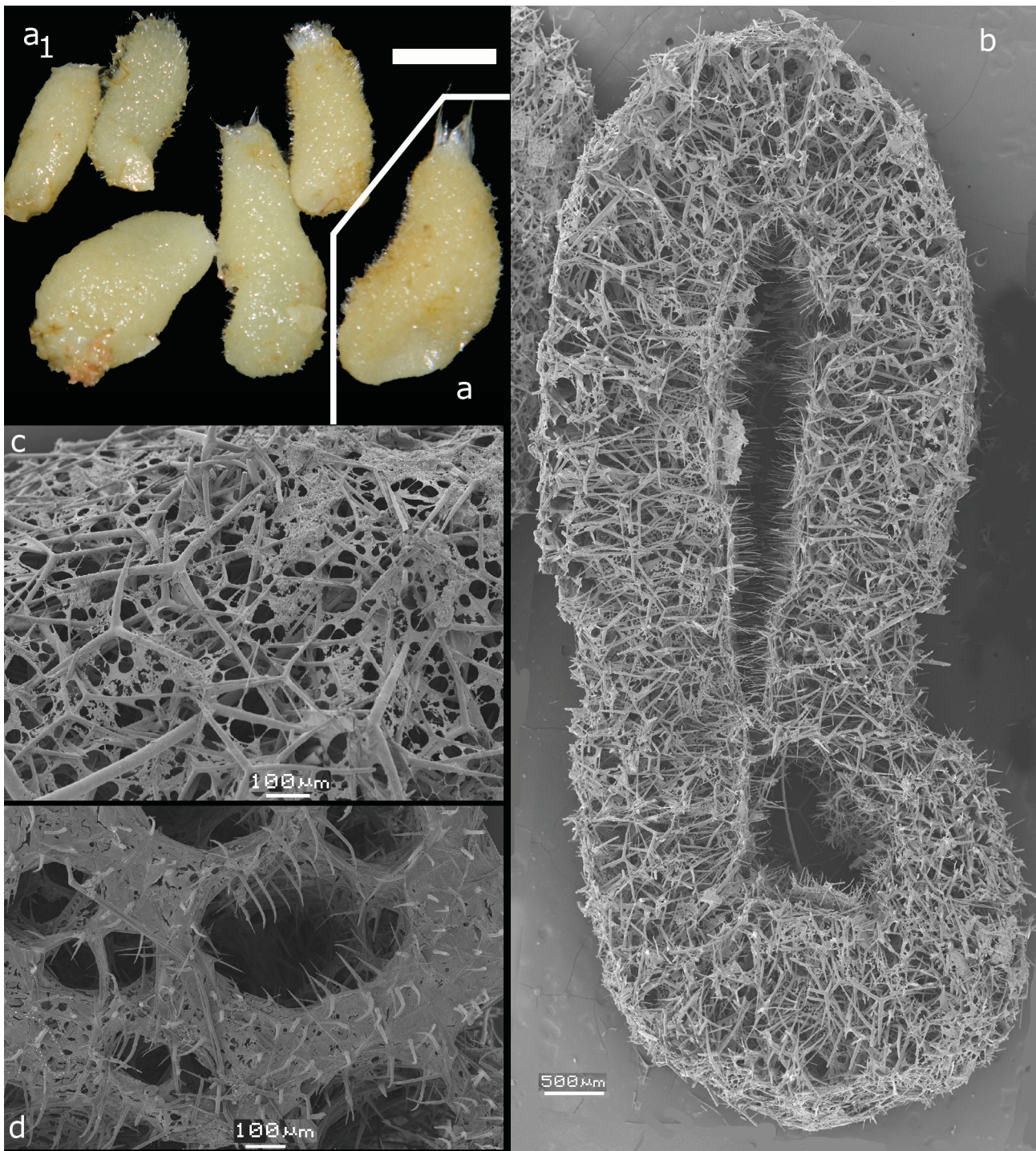


FIGURE 83. *Paraleucilla erpenbecki* sp.nov., a, habitus holotype ZMA Por. 22409a, from the Mozambique Channel, a1 habitus of paratypes ZMA POR. 22409c, from the same location (scale bar = 1 cm), b–d, SEM images of skeleton, b, cross section, c, overview from above of peripheral skeleton, d, overview from above of atrial skeleton.

The new species is close to West Australian *Paraleucilla princeps* (Row & Hôzawa, 1931) (as *Leucilla princeps*, p. 799, pl. 21 fig. 17, text-fig. 16), sharing tubular shape and most of the spicule complement. Also the sizes of the spicules conform rather closely. A major difference is the absence of giant triactines in the choanosomal skeleton. These spicules are a dominant feature of the present species, forming the skeletal structure of the peripheral inarticulate skeleton together with the apical actines of the subcortical tetractines. Row & Hôzawa do mention the presence of similar shaped smaller triactines but these only occur in the oscular region. Also not present are the small diactines.

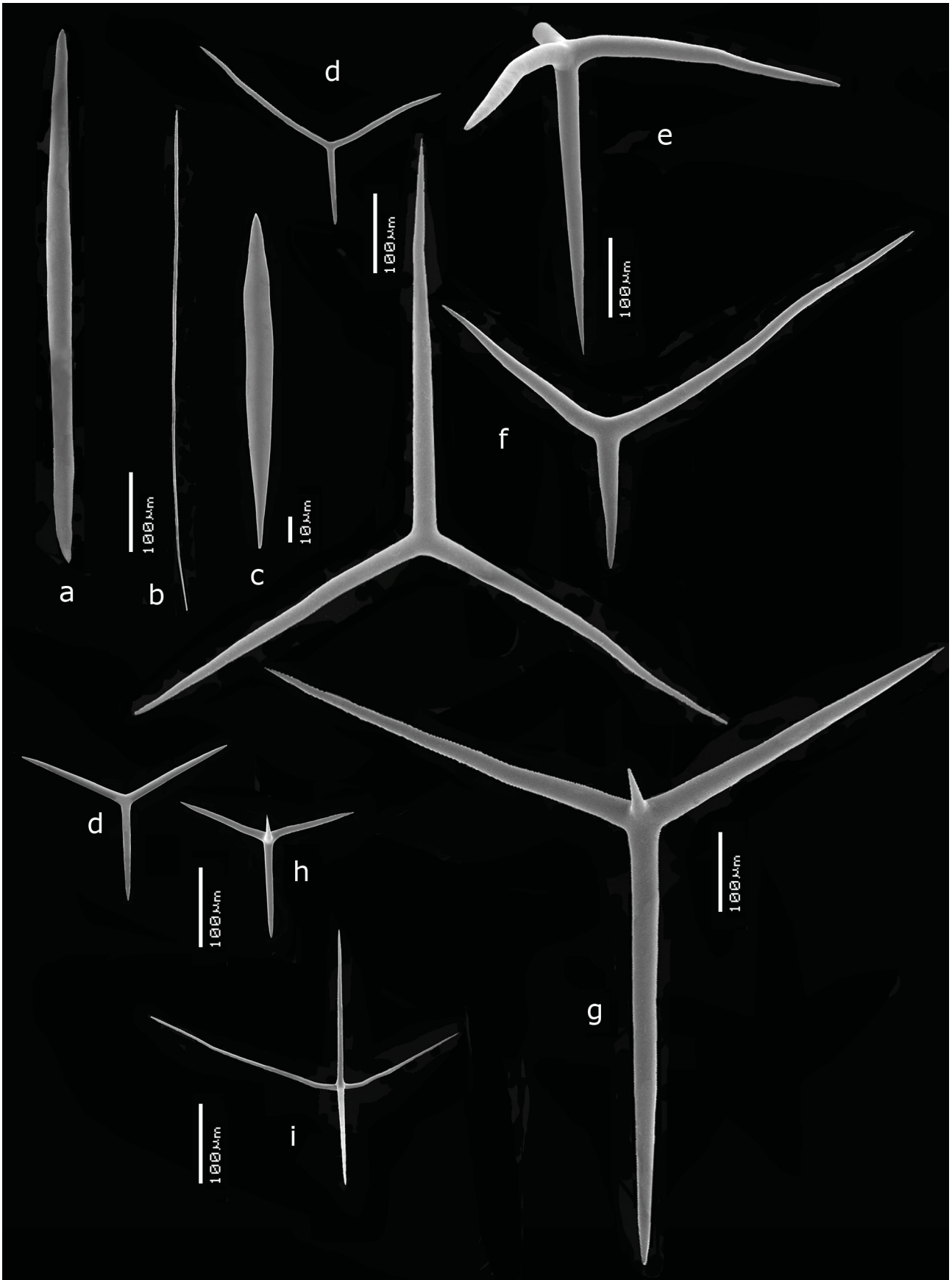


FIGURE 84. *Paraleucilla erpenbecki* sp.nov., ZMA Por. 22409a, SEM images of the spicules, a, giant diactine, b, trichoxea fragament, c, rare microdiactine, d, cortical and atrial triactines, e, (sub)cortical tetractine, f, giant choanosomal triactines, g, giant choanosomal tetractine, h, subatrial tetractine, i, atrial tetractine.

Paraleucilla dalmatica Klautau *et al.* 2017 from the Mediterranean is similar in shape and skeletal structure, but spicule sizes differ significantly. Also, Brazilian *P. incomposita* Cavalcanti *et al.* 2014 is close in shape and structure but differs also in spicule sizes. Recently (Chagas & Cavalcanti 2017), it was discovered that this species possesses choanosomal pentactines as a remarkable unique feature.

We obtained a 28S partial gene sequence for the holotype and compared it with a sequence downloaded from GenBank of Mediterranean *Paraleucilla* spec. (supposedly the same as *P. magna* Klautau *et al.*, 2004), which grouped together in our Phylogeny of Fig. 3 at a moderate bootstrap frequency (77%). From a separate investigation of a trimmed alignment of 295 sites obtained for the two sequences we found that *P. erpenbecki* sp.nov. differs in 8 sites from the Mediterranean *Paraleucilla* spec.

Family Lelapiidae Dendy & Row, 1913

Genus *Kebira* Row, 1909

Remark. Up until now, the genus *Kebira* is monotypical and restricted to the Red Sea (Row 1909; Burton 1952; Ilan & Vacelet 1993; Borojević *et al.* 2000, 2002b). The skeleton of the so far only species, *K. uteoides* Row, 1909 is characterized by the possession of tracts of peculiar ‘nail-shaped’ triactines, in addition to giant diactines and two forms of sagittal triactines. We also encountered specimens of this species at Jeddah in the Saudi Arabian part of the Red Sea (see below). However, sponges with the spicule complement mentioned above, including the ‘nail-shaped’ triactines, are here reported from outside the Red Sea, viz. Eastern South Africa and the Seychelles. The similarity of these specimens with Red Sea *Kebira uteoides* is considerable, but the atrial spicules (exclusively sagittal triactines with short unpaired actine in the Red Sea *Kebira*’s) include also similarly shaped sagittal tetractines with short conical apical actines. We propose to distinguish the South African tetractine-bearing specimens as a separate species of *Kebira*, described below. The specific status of the small tetractine-bearing specimen from the Seychelles is kept undecided because of considerable differences with the new species.

Kebira uteoides Row, 1909

Figs 85a–g, 86a–e

Kebira uteoides Row, 1909: 210, pl. 20 figs 8–9, text-figs 7–8; Burton 1952: 164; Ilan & Vacelet 1993: 110, figs 2–4.

Material examined. RMNH Por. 9563, Saudi Arabia, Jeddah, near Thuwal, Al Fahal N, 22.300194°N 38.959583°E, depth 12 m, coll. N.J. de Voogd, scuba, field nr. THU04/JED052, 8 November 2014; RMNH Por. 9664, Saudi Arabia, Jeddah, near Thuwal, Um Albalam, 22.193556°N 38.9475°E, depth 15 m, scuba, coll. N.J. de Voogd, field nr. THU10/JED168, 12 November 2014.

Description. Squat, laterally flattened, irregularly tubular individuals (Figs 85a–d), attached to vertical walls and hanging down from the ceiling of cavities, with large apical or lateral oscules. In life (Figs 85a,c), colors are shades of grey and pinkish white, on deck (Figs 85b,d) and in preservation they become yellow. Size up to 4 cm high, and 5 x 3 cm in lateral expansion. Oscules 4–6 mm in diameter. Surface smooth. Consistency firm to hard.

Aquiferous system. Leuconoid.

Skeleton. (Figs 85e–g) In cross section (Fig. 85e), there is a cortical skeleton of sagittal triactines, mostly with long unpaired actines (Fig. 85f), carried by tangentially arranged giant diactines. Underneath, the choanosomal skeleton is formed by perpendicular giant diactines, tracts of nail-shaped triactines (arrows in Fig. 85e) and large sagittal triactines with long unpaired actines. The atrial skeleton (Fig. 85g) is predominantly formed by sagittal triactines with short unpaired actines.

Spicules. (Figs 86a–e) Giant diactines, nail-shaped triactines, sagittal triactines, microdiactines.

Giant and smaller diactines (Fig. 86a), fusiform, symmetrical, sharply pointed, in a wide size range, 540–1489–2022 x 25–79–108 µm.

Nail-shaped triactines (Figs 86b,b1), thinly fusiform, pointed at one end, at the opposite end provided with two conical actines arranged at a slight angle, in a large size range, unpaired actines 105–317–477 x 5.5–8.5–10 µm, paired actines 3–7 x 3 µm.

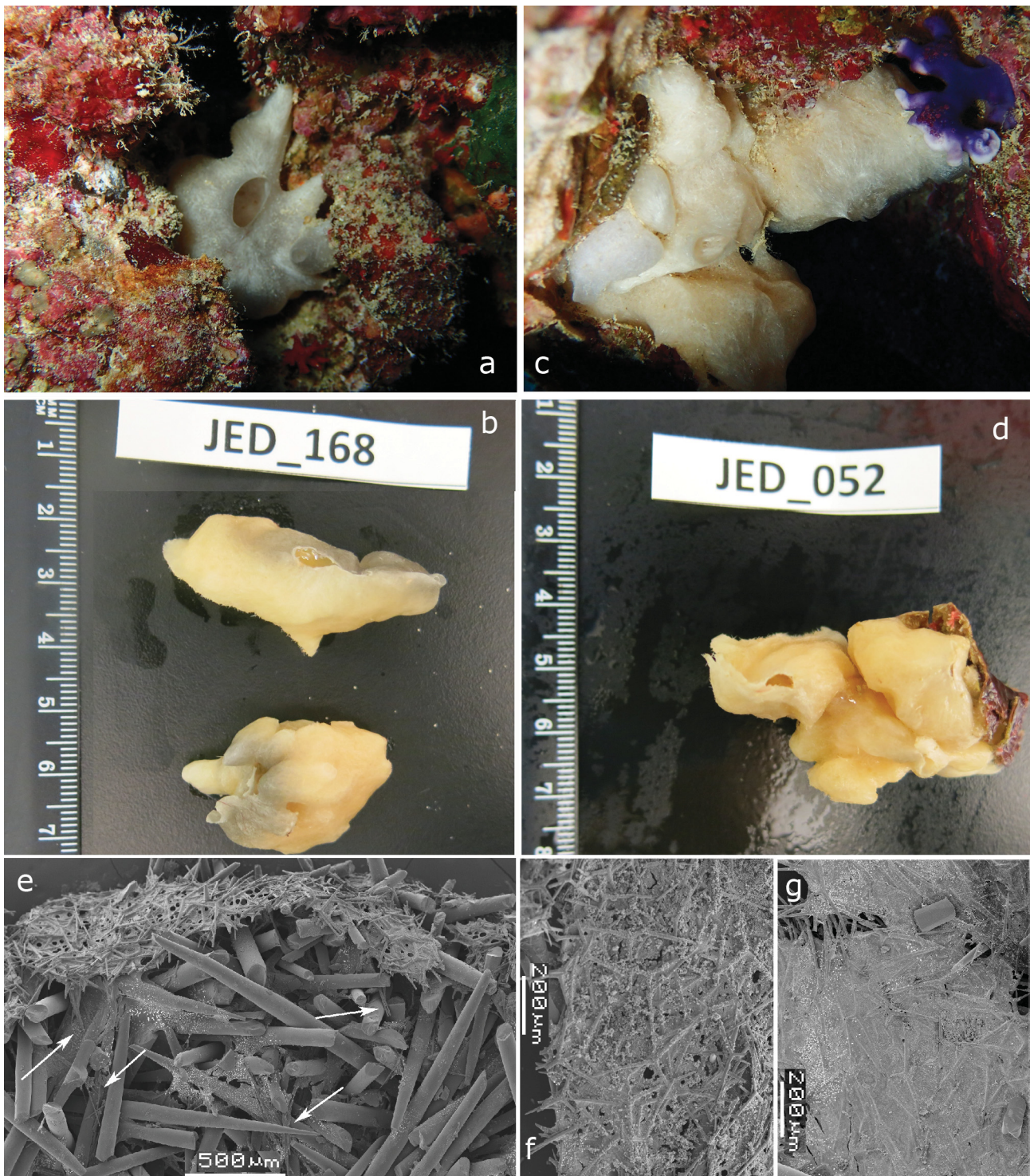


FIGURE 85. *Kebira uteoides* Row, 1909, a, habitus in situ of RMNH Por. 9664, from Jeddah (Saudi Arabia), b, the same on deck, c, habitus in situ of RMNH Por. 9563, from Jeddah (Saudi Arabia), d, the same on deck (photos N.J. de Voogd), e–g, SEM images of skeleton of RMNH Por. 9664, e, cross section, f, overview from above of peripheral skeleton, g, overview from above of atrial skeleton.

Large sagittal triactines (Fig. 86c), with long unpaired actines, and flaring paired actines; unpaired actines 306–371–462 x 7–7.9–8.5 μm , paired actines 204–227–248 x 9–10.4–12 μm .

Atrial sagittal triactines (Figs 86d) with short unpaired actines and straight paired actines; unpaired actines 57–86–121 x 8.5–10.1–12 μm , paired actines 179–228–282 x 11.5–13.9–17 μm .

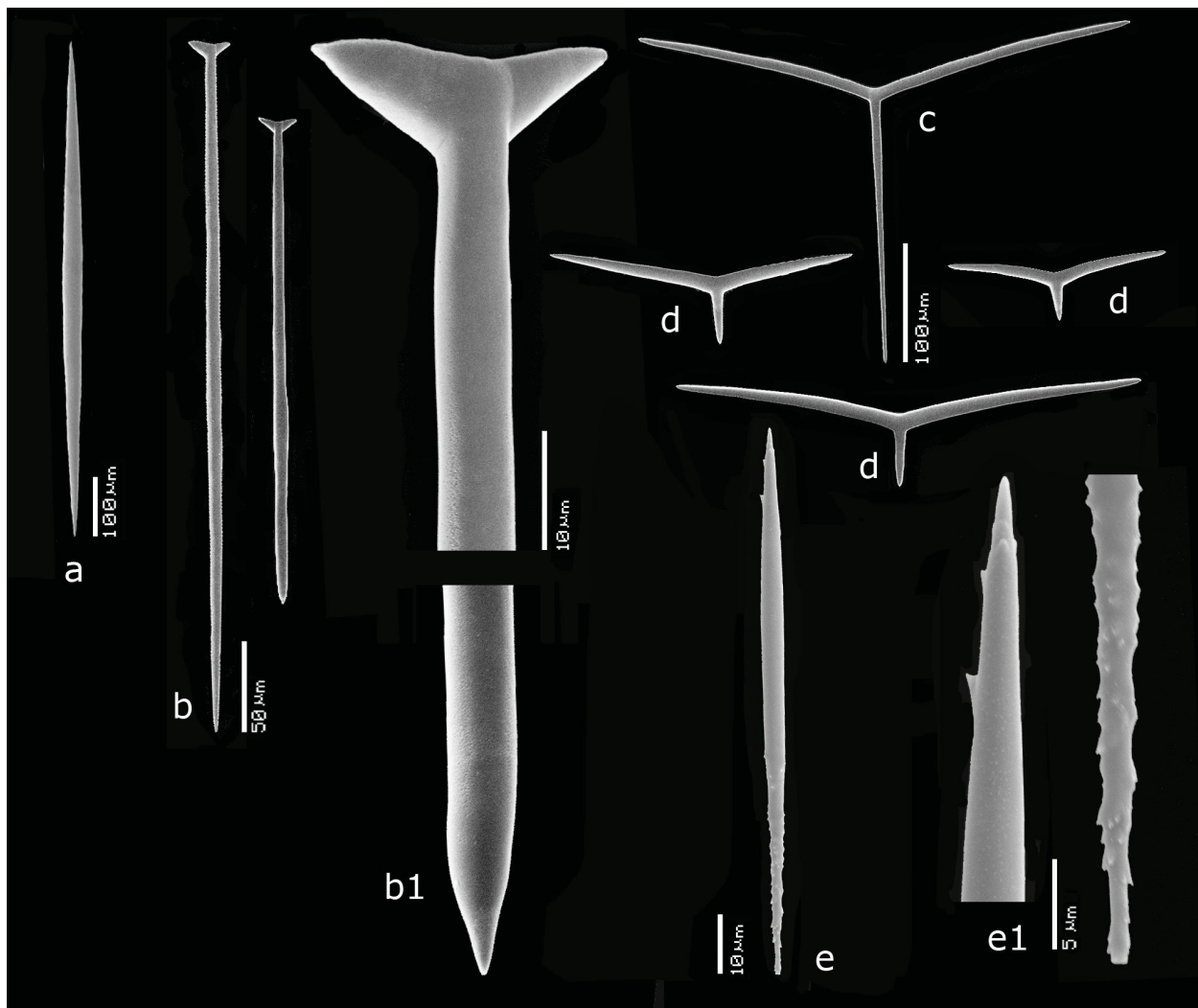


FIGURE 86. *Kebira uteoides* Row, 1909, RMNH Por. 9664, SEM images of the spicules, a, giant diactine, b, nail-shaped triactines, b1, detail of nail-shaped triactine, c, triactine with long unpaired actine, d, triactines with short unpaired actines, e, microdiactine (not previously reported, so perhaps not proper), e1, details of both ends of microdiactine.

Small thin diactines with tiny spines at both ends (Figs 86e,e1), rare, not certainly proper to the sponge, but sufficiently characteristic to be a possible, previously unobserved, spicule type, 51–102 x 2–7 µm.

Distribution and ecology. Northern Red Sea: Gulf of Suez, Egypt (Sharm-al-Sheik), Saudi Arabia (Jeddah), hanging down in caves on shallow water reefs.

Remarks. The only noteworthy difference with Row's description of the type specimen is that he confused the position of the cortical and the atrial sagittal triactines. It can be clearly seen in our Fig. 85g, showing the atrial surface, that the predominant spicule type is the sagittal triactine with short unpaired actine. In Figs 85e (upper part) and f, the dominant spicule type is the long-shafted sagittal triactine clearly visible. Our spicule sizes are more or less the same as in Row's specimen, although we did not observe giant diactines of 4 mm length.

The small spined diactines may or may not be proper to the sponge.

Burton (1952) did not give a description other than mentioning that his specimen from Sharm al Sheik (Egypt) was 2 cm high.

Ilan & Vacelet (1993) found giant diactines up to 4 mm, but omitted further spicule measurements, concentrating on a description of the soft parts.

We obtained partial 28SrRNA sequences for the two specimens. In our Phylogeny of Fig. 3, these grouped along with the new *Kebira* species described below in a larger clade together with *Ute ampullacea*, *Paragraptia waguensis* Hôzawa, 1940, and *Grantiopsis heroni* Wörheide & Hooper, 2003. These species were added to our analysis to confirm the affiliation of *Kebira*. The position of *Ute ampullacea* (cf. also above) in the group is

surprising, but *Kebira*, *Grantiopsis* and also *Paragrastia* (see Van Soest *et al.* 2015) are likely members of the family Lelapiidae.

***Kebira tetractinifera* sp.nov.**

Figs 87a–d, 88a–f, 89a–e

Material examined. Holotype, ZMA Por. 15245, South Africa, Port Elizabeth, Sea View, 32.9333°S 27.7°E, coll. A. van Schie, field nr. UPES 96–074, 6 February 1998.



FIGURE 87. *Kebira tetractinifera* sp.nov. from Eastern South Africa, a, habitus of holotype ZMA Por. 15245 (scale bar = 1 cm), b, habitus of paratype ZMA Por. 13952 (scale bar = 1 cm), c, detail of the same, d, light microscopic image of cross section of body wall of holotype.

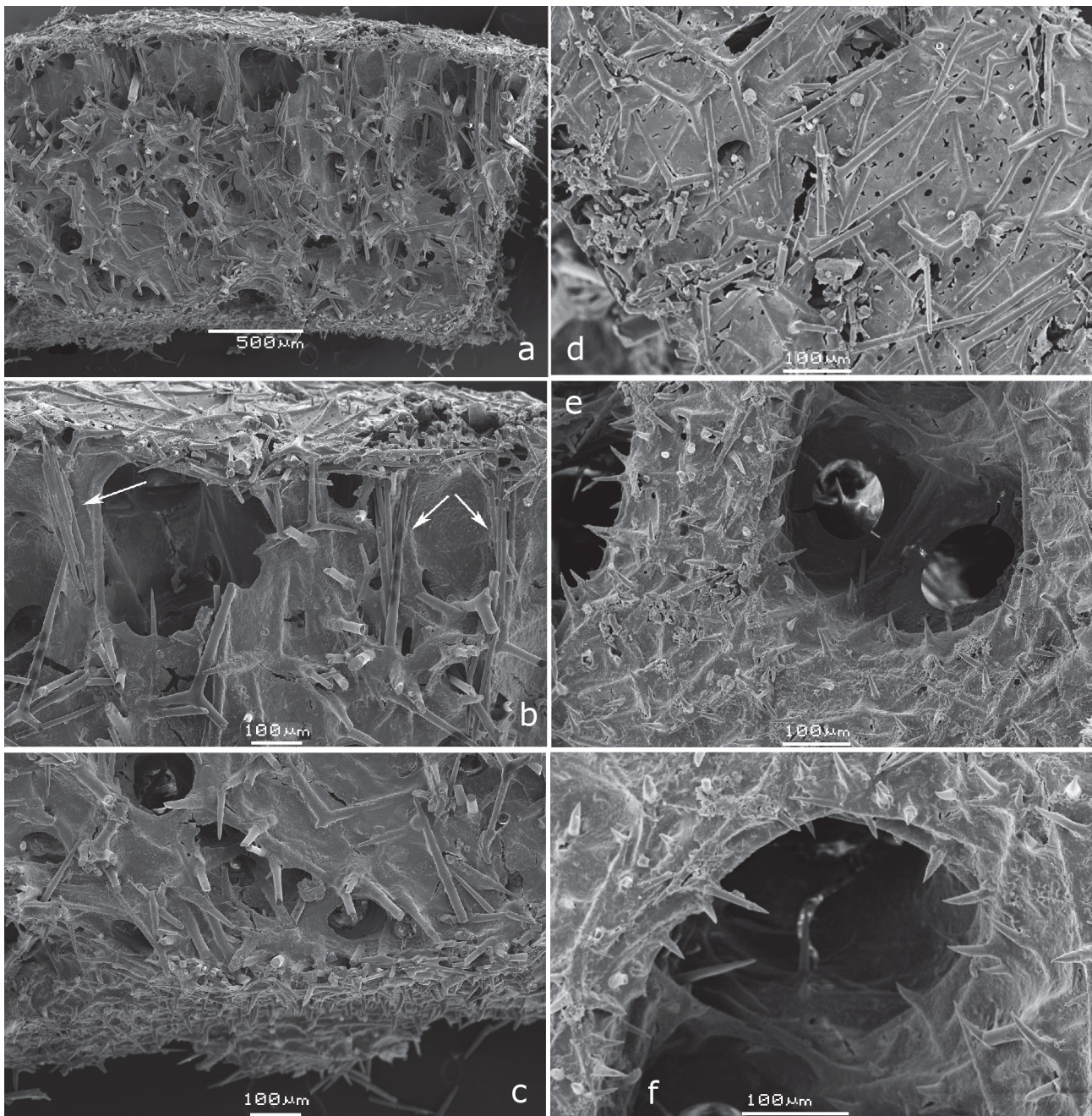


FIGURE 88. *Kebira tetractinifera* **sp. nov.**, holotype ZMA Por. 15245, SEM images of sections of the skeleton, a, cross section of body wall, b, detail of cross section of peripheral skeleton (arrows: tracts of nail-shaped triactines), c, detail of the cross section of the atrial skeleton, d, overview from above of peripheral skeleton, e, overview from above of atrial skeleton, f, detail of the atrial skeleton with protruding apical actines of the tetractines with short unpaired actines.

Paratype, ZMA Por. 13952, South Africa, Port Elizabeth, Cape Recief, coll. H. Engel, 20 November 1938.

Description. A mass of upright tubular shapes, connected by flattened ridges. The holotype (Fig. 87a) is wet (alcohol preservation) and has a light beige color and a smooth surface. Size of the entire specimen is 3 x 2 x 2 cm, tubular individuals about 0.5 cm diameter. The paratype (Figs 87b–c) is a dried tubular individual of 4 cm high, pale yellow in color, with a broad base and a diameter of 1 cm, with atrial wall 2 mm thick and atrial cavity 5 mm in diameter. Consistency firm to hard.

Aquiferous system. Leuconoid.

Skeleton. (Figs 87d, 88a–f) In a cross section of the wall (Figs 87d, 88a–c), there is a cortical skeleton (Fig. 88d) formed by triactines with longer unpaired actines, carried by the pointed ends of perpendicular giant diactines, with only few of the diactines in a tangential position. The choanosomal skeleton is a dense mass of large triactines

partitioned off by giant diactines and thin tracts of nail-shaped triactines (arrows in Fig. 88b). The atrial skeleton is a layer of sagittal tri- and tetractines with short unpaired actines, with the apical actines of the tetractines protruding into the atrial cavity (Figs 88c,e–f).

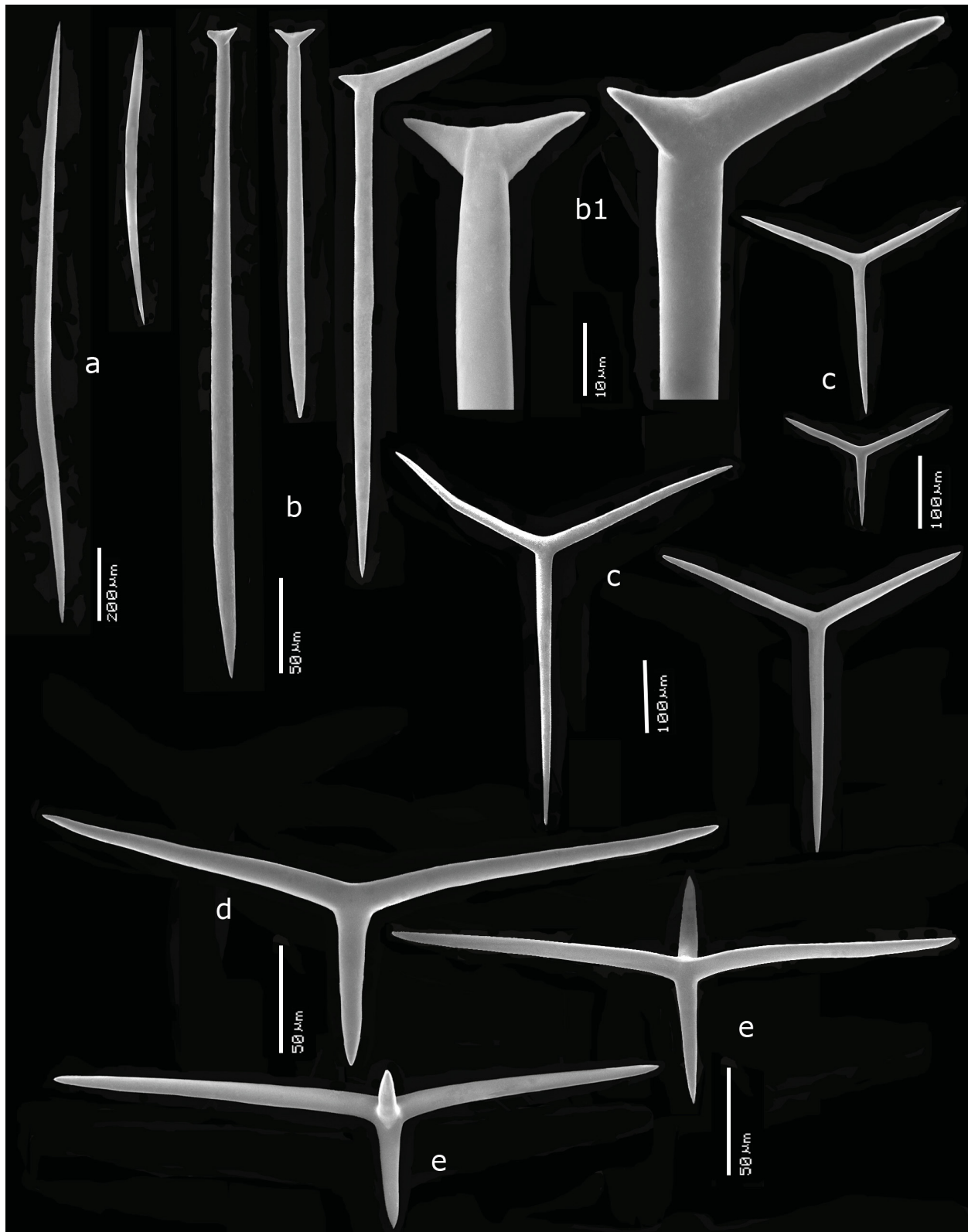


FIGURE 89. *Kebira tetractinifera* **sp.nov.**, holotype ZMA Por. 15245, SEM images of the spicules, a, giant and smaller diactines, b, nail-shaped triactines, b, details of nail-shaped triactines, c, triactines with long unpaired actines, d, triactine with short unpaired actine, e, tetractines with short unpaired actines.

Spicules. (Figs 89a–e) Giant diactines, nail-shaped triactines, triactines with long unpaired actines, triactines with short unpaired actines, tetractines with short unpaired actines.

Giant and smaller diactines (Figs 89a), fusiform, curved, 400–904–1380 x 15–33.8–45 μm .

Nail-shaped triactines (Figs 89b,b1), fusiform shaft, one end pointed, the opposite with conical or further extended short actines, arranged under a slight angle, often asymmetrical, unpaired actines 155–249–352 x 7.5–9.7–14 μm , paired actines 4–14.5–40 x 4–7.5–12 μm .

Triactines with long unpaired actines (Figs 89c), usually sagittal with paired actines similar in length or shorter, occasionally equiangular eiradiate; unpaired actines 156–260–355 x 10–15.4–22 μm , paired actines 115–182–256 x 7–14.2–20 μm .

Triactines with short unpaired actines and straight paired actines (Fig. 89d); unpaired actines 49–76–100 x 8–9.8–12 μm , paired actines 155–169–195 x 7.5–9.9–11 μm .

Tetractines with short unpaired actines and straight paired actines (Figs 89e); unpaired actines 58–82–115 x 8–9.1–10 μm , paired actines 126–151–181 x 7–8.9–10 μm , apical actines 32–43.6–50 x 6–7.6–10 μm .

Distribution and ecology. Port Elizabeth region, Eastern South Africa, in shallow water.

Etymology. The name reflects the presence of sagittal tetractines, a feature distinguishing the new species from the type species, *K. uteoides*.

Remarks. The possession of tetractines is the defining character of the new species, but the diactines differ from *K. uteoides* in being shorter and thinner and not forming a thick cortical layer. Less definite is the difference in thickness of the triactines with long unpaired actines, with those of *K. uteoides* being measurably thinner. See also below in the description of the Seychelles *Kebira* specimen.

We obtained partial 28S sequences for the two Red Sea specimens of *K.uteoides* and the holotype of *K. tetractinifera* **sp.nov.** They grouped together in our Phylogeny of Fig. 3 with a high bootstrap value (94%). A separately investigated trimmed alignment of these three sequences, totaling 400 sites, showed four site differences between the two identical *K. uteoides* sequences and the sequence of the new species.

***Kebira* spec.**

Figs 90a–g

Material examined. ZMA Por. 10379b, Seychelles, Mahé, E coast, N of Moyenne Island, 4.6167°S 55.5167°E, depth 1–7 m, reef, snorkeling, coll. R.W.M. van Soest, field nr. NIOP-E stat. 606, 10 December 1992.

Description. The specimen is small and tubular (Fig. 90a), about 1.5 cm high, 0.5 cm in diameter, with a narrow apical oscule. Color in alcohol dirty white. Surface smooth and shining, due to a thick surface armor of tangential giant diactines.

Aquiferous system. Leuconoid.

Skeleton. In cross section there is a thin cortical layer of triactines with long unpaired actines carried by a thick mass of tangentially arranged giant diactines. The choanosome is a mass of triactines traversed in places by short tracts of nail-shaped triactines. The atrial skeleton is a layer of tri- and tetractines with short unpaired actines and straight paired actines.

Spicules. (Figs 90b–g) Giant diactines, nail-shaped triactines, large triactines with long unpaired actines, small tri- and tetractines with short unpaired actines.

Giant and smaller diactines (Figs 90b), fusiform, curved, 105–869–2520 x 7.5–37.1–84 μm .

Nail-shaped triactines (Figs 90c,c1), fusiform, with one end pointed and the opposite end with two tiny actines, usually more or less symmetrical; unpaired actine 252–503–781 x 8.5–9.9–12 μm , paired actines 3–6.8–15 x 2.5–4.2–6 μm .

Triactines with long unpaired actines and flaring paired actines (Fig. 90d); unpaired actines 292–348–384 x 10–17.8–24 μm , paired actines 226–297–342 x 9–18.4–23 μm .

Tetractines (Fig. 90e), with short unpaired actines and straight paired actines; unpaired actines 31–49–61 x 8–10.3–12 μm , paired actines 69–192–231 x 8–11.6–14 μm , apical actines 3–25–32 x 3–7.9–10 μm .

Triactines (Fig. 90f), with short unpaired actines and straight paired actines; unpaired actines 30–46–63 x 7–10.3–12 μm , paired actines 71–188–234 x 8–10.9–12 μm .

Distribution and ecology. Seychelles, shallow-reef locality.

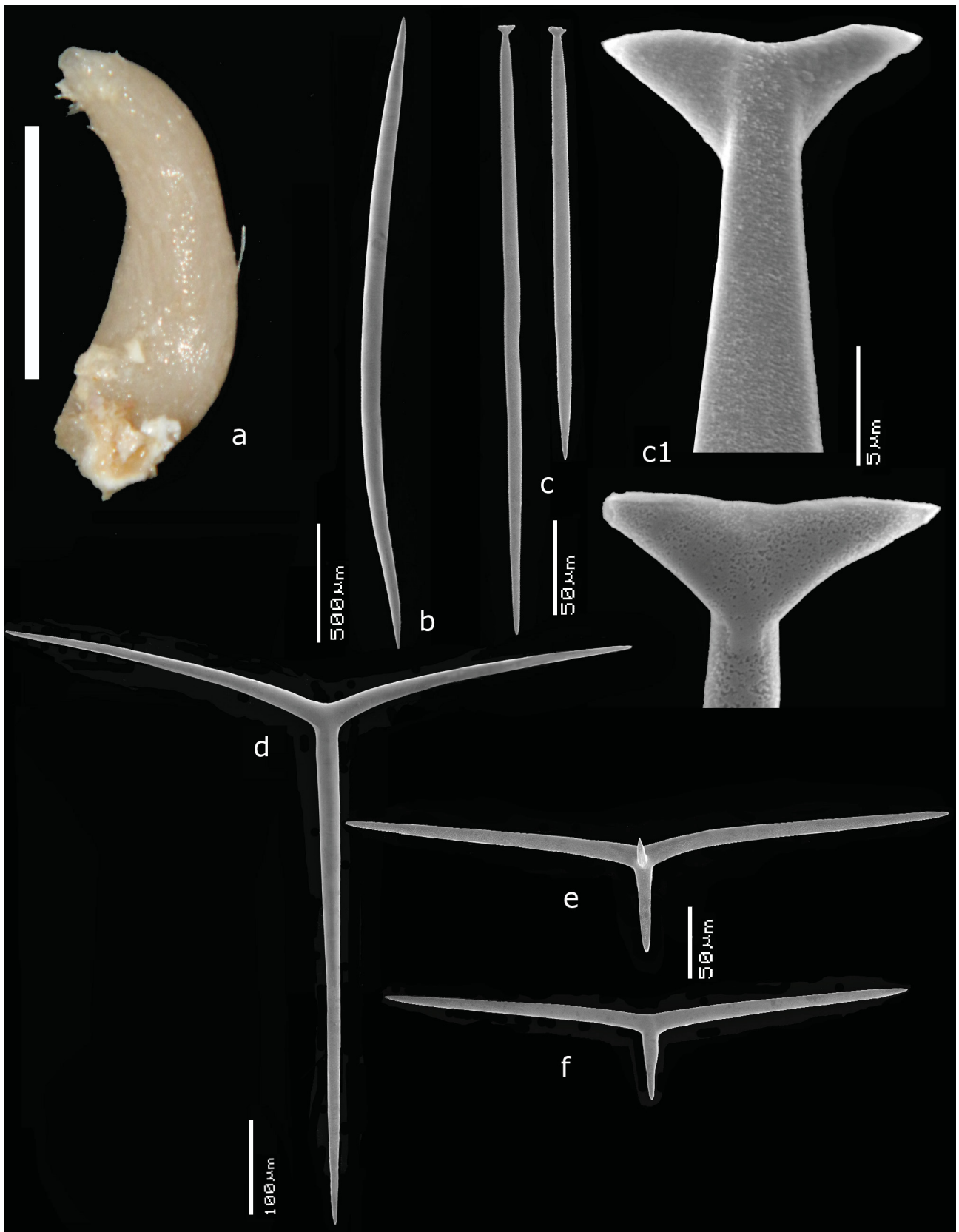


FIGURE 90. *Kebira spec.*, ZMA Por. 10379b, from the Seychelles, a, habitus (scale bar = 1 cm), b–f, SEM images of the spicules, b, giant diactine, c, nail-shaped triactines, c1, details of nail-shaped triactines, d, large triactine with long unpaired actine, e, tetractine with short unpaired actine, f, triactine with short unpaired actine.

Remarks. Although this specimen shares the possession of atrial tetractines with *Kebira tetractinifera* **sp.nov.**, it shares also features with *K. uteoides* such as a dense layer of tangential diactines, twice as long as those of *K. tetractinifera* **sp.nov.** Further research is necessary to establish the value of these features for distinction of additional taxa in *Kebira*.

Unfortunately, our attempt to obtain a 28S sequence of the specimen failed.

Order Baerida Borojević *et al.*, 2000

Family Trichogypsiidae Borojević *et al.*, 2000

Genus *Trichogypsia* Carter, 1871

Trichogypsia spec.

Figs 91a–e

Material examined. Microscopic slide ZMA.POR.P1616, Seychelles, NE of Aride Island, 4.2°S 55.6833°E, depth 40 m, coll. R.W.M. van Soest, field nr. NIOP-E stat. 715, 19 December 1992. Unfortunately, the specimen, from which the slide was made, has not been found again in the collections. The data provided here are meant to draw attention to the existence in the Western Indian Ocean of a species of this rare and peculiar genus.

Description. A thin red encrustation, lateral size 6 x 5 mm, thickness 2 mm. Surface microconulose.

Aquiferous system. Leuconoid.

Skeleton (Figs 100a–e) In cross section (Fig. 100a) there is a cortical region consisting of a palisade of smaller diactines, forming small bouquets of 6–10 spicules (Figs 100b–c), with sharp points directed outward. The cortical palisade is carried by tangential larger diactines. The choanosome has large hollows (Fig. 100a), interpreted as wide canals, but not provided with special atrial skeleton. The main skeleton consists of vague tracts of larger diactines (Fig. 100d–e).

Spicules. Asymmetrical diactines, in two distinct forms. The cortical palisade has smaller diactines (Fig. 100d), often wobbly or crooked, with the outward-directed end sharply pointed, and the inward-directed end bluntly rounded with spines and small warts, 121–147–192 x 8–10.9–14 µm. The main skeleton consists of larger diactines (Fig. 100e), lightly spined along the entire shaft, more heavily spined at the bluntly rounded ends, 315–426–530 x 11–15.4–18 µm.

Distribution and ecology. Seychelles, at 40 m depth.

Remarks. The genus *Trichogypsia* is so far confined to the North Atlantic and North Pacific. Following Dendy & Row (1913), the World Porifera Database (Van Soest *et al.* 2018) recognizes three distinct species. In the North Atlantic there are Southern England's *T. villosa* Carter, 1871 and Southern Norwegian *T. incrustans* (Haeckel, 1872), originally as *Leucyssa*. This contrasts with Burton's (1963) opinion that the two are conspecific. Borojević *et al.* (2000) have re-examined only Carter's (1871) slide, remarking that the internal canals are lined by special curved spicules, not noted by Carter. In the absence of a redescription of Haeckel's material, we remain in doubt over the specific differences. Recently, Lehnert & Stone (2017) described a further species *Trichogypsia alaskensis* from the S coast of Alaska. In any case, *T. villosa* and *T. incrustans* (greyish white or greenish white) and *T. alaskensis* (golden brown) differ from the Seychelles specimen (red) in life color. Spicule lengths of the present specimen are 120–530 µm, Carter and Haeckel give 200–450 µm for the two European species, so these match closely. *T. alaskensis* has much larger spicules, up to 1225 x 46 µm.

Additional Western Indian Ocean and Red Sea Calcarea

The species mentioned below have been reported from the various parts of the Western Indian Ocean covered in this paper. Since we did not have material from the mainland coast of India, nor from Western Australia, we will not list and discuss species from these areas. We divided up the additional records of the region into Red Sea, Arabian Sea, Seychelles & Mascarene Islands, East Africa, Madagascar and Mozambique Channel, and South Africa westwards until 25°E.

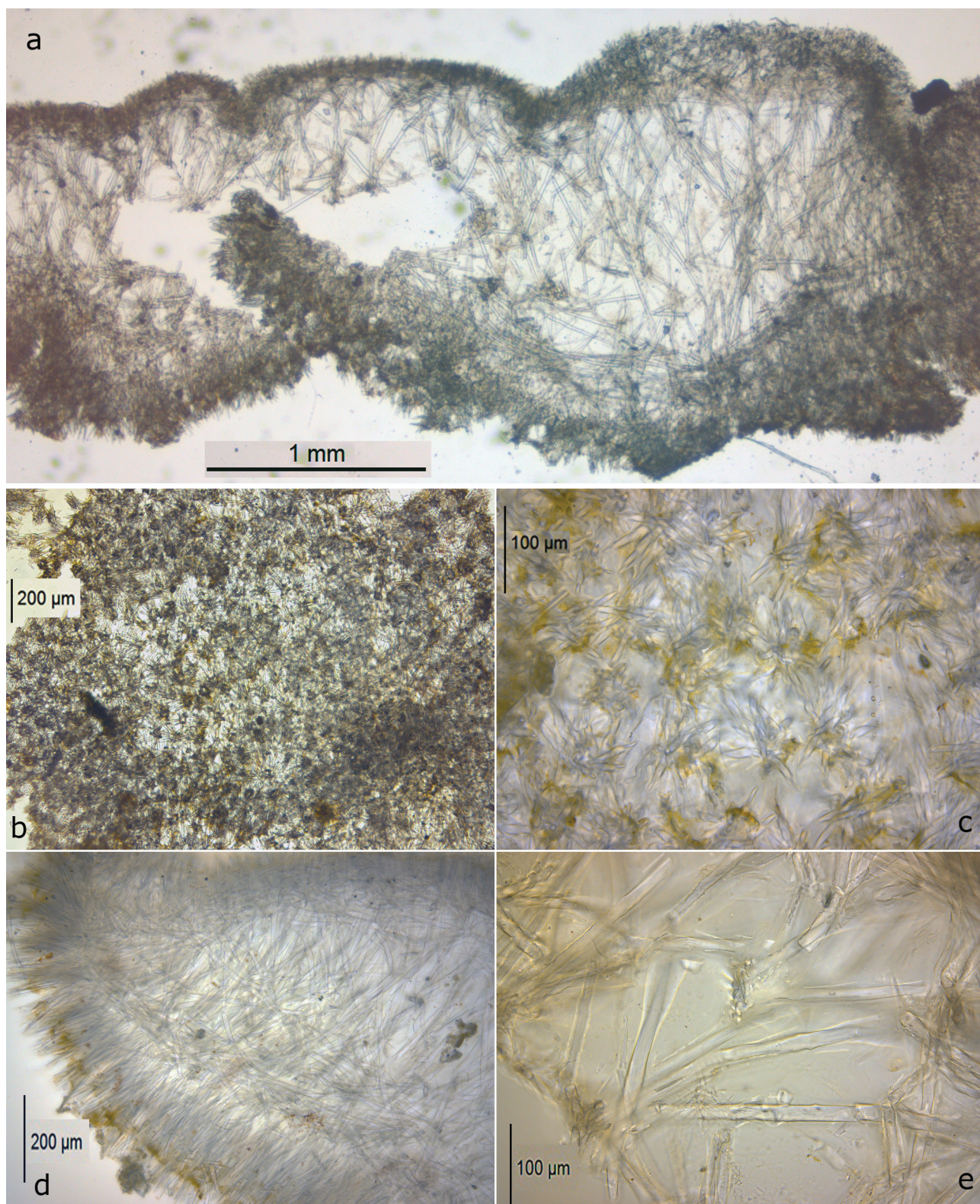


FIGURE 91. *Trichogypsia* spec., slide ZMA.POR.P1616, from the Seychelles, a, cross section, b, overview of surface, c, detail of bouquets cortical diactines, d, cross section of peripheral and choanosomal skeleton, e, detail of choanosomal skeleton.

Many of the specimens reported below are kept in the Natural History Museum, London, including slides. We were unable to examine these, except for a few. A future continuation of the study of the taxonomy of *Calcarea* of the region might benefit from a visit to these collections.

Red Sea

Clathrina rotundata Voigt *et al.*, 2017

Recently described extensively in Voigt *et al.* 2017 and discussed above in the Remarks of *C. maremeccae* **sp.nov.**

Clathrina primordialis sensu Row 1909

No description has been given by Row (1909: 184). Voigt *et al.* 2017 suggested it is likely conspecific with *Clathrina rowi*. The original description by Haeckel (1872) (vol. 2: 16, as *Ascetta*) is from the Mediterranean. See also below in the paragraph of additional East African Calcarea).

Leucosolenia canariensis sensu Burton 1952

The specimen was greyish white and 10 cm in diameter, but there is no further description and the identity remains uncertain. The original description by Miklucho-Maclay (1868: 230, as *Nardoa*) is from the Canary Islands.

Clathrina tenuipilosa sensu Row 1909

Although Row's (1909: 185) description contains many words, there are no measurements of the spicules. He describes 'oxeas of such unusual and constant form, being very long and extremely slender', and mentions tetractines, from which we may conclude that it is possible the identification is correct. The species has originally been described by Dendy (1905) from Sri Lanka, and it has been transferred to *Arturia* by Klautau *et al.* (2013). Burton (1952) reported this species from the Egyptian part of the Gulf of Aqaba (as *Leucosolenia*), giving their size (up to 3 cm), but failing to describe the skeleton and the spicules.

Soleneiscus hamatus Voigt *et al.*, 2017

This was recently described and for its properties the reader is referred to Voigt *et al.*'s paper.

Leucandra aspera sensu Row 1909

Row (1909: 186) mentioned 'a considerable number of fragments', but failed to give taxonomic details. The original description of Schmidt (1862: 15, as *Sycon asperum*) is from the Adriatic. This record remains *incertae sedis*.

Leucandra primigenia sensu Row 1909

This has not been described, only listed by Row (1909: 186), so it remains *incertae sedis*. *Leucetta primigenia* Haeckel, 1872 is a species from the Adriatic, unlikely to occur in the Red Sea.

Leucaltis bathybia Haeckel, 1872

Next to Haeckel's (1872: 156) description, there are three additional records, (1) by Row (1909: 205) from Suez as *Leucilla bathybia*, (2) by Burton (1952: 164) from the Gulf of Aqaba as *Leuconia*, and (3) by Lévi (1965: 25) from the southern Red Sea, also as *Leuconia*. Neither Row nor Lévi provided a description, so we cannot comment. Burton (1952) gave a partial description, which may indicate his specimens belonged to *Paraleucilla crosslandi* (see above in the remarks of that species). The species as described by Haeckel (1872: 156) is also discussed above under *Leucaltis nodusgordii* and under *Paraleucilla crosslandi*. Its identity remains to be decided from redescription of the type material, ZMB 326.

Leuconia nausicaae sensu Burton 1952

The Mediterranean species *Leucaltis nausicaae* Schuffner, 1877 was reported from the Egyptian part of the Gulf of Aqaba by Burton (1952) as *Leuconia*, but he failed to give a description. Schuffner's species is considered a *Leucandra*, so we assume that Burton's record also concerns a *Leucandra*. It likely does not possess giant diactines and has atrial tetractines, which makes it similar to *Leucandra pilula* **sp.nov.**, but this needs further corroboration.

Syconella proboscidea Haeckel, 1870

This combination is a clear *nomen nudum* as there is no description given in Haeckel's 1870 paper (p. 239). In the 1872 monograph, Haeckel reassigned the name *proboscidea* to *Sycandra* Haeckel, 1872. Since then this genus is

restricted to a single species *S. utriculus* (Schmidt, 1869) (originally as *Ute* Schmidt, 1862). Most other *Sycandra* species are assigned to *Sycon* Risso, 1870 and from the few remarks of Haeckel (1872: 313) it is likely that *Sycandra proboscidea* is also a member of that large genus. *Sycon proboscidea* (Haeckel, 1872) from the Egyptian Red Sea (Siemens collection) is poorly known and no recent records are available. It is a *species inquirenda*.

***Sycon coronatum* sensu Row 1909**

Other than the size of the specimen and its fringe, Row (1909: 185) has not described this material. This European species described by Ellis & Solander 1786 (as *Spongia*) is considered a junior synonym of *S. ciliatum* (Fabricius, 1780). It is unlikely that the Red Sea specimen belongs to that species. This record remains *incertae sedis*.

***Sycon raphanus* sensu Row 1909**

No description has been given by Row (1909: 185). The species, originally described by Schmidt (1862), is Mediterranean. We assume that the Red Sea material belongs to a different species, remaining *incertae sedis*.

***Grantessa glabra* Row, 1909**

See Row (1909: 203, pl. 19 figs 5–6, text fig. 4). Discussed above in connection with possible synonymy with *Sycettusa stauridia* (Haeckel, 1872). The type specimen BMNH 1912.2.1.9 was re-examined by us. It is a small tube with side oscule. It has cortical and atrial triactines much larger (400–700 µm) and diactines and pseudosagittal triactines much thicker (50–90 µm) than Haeckel's and the above described material. For the time being it is reassigned to *Sycettusa glabra*, but redescription is necessary. Burton (1952) reported this species from the Egyptian part of the Gulf of Aqaba without a description.

Arabian Sea

Burton (1959) reported a number of species but provided no descriptions. We re-examined several specimens in the Natural History Museum, London.

Leucosolenia gardineri Dendy, 1913 sensu Burton (1959), not re-examined.

Grantessa glabra Row, 1909 sensu Burton (1959): not re-examined.

Grantessa sycilloides Schuffner, 1877 sensu Burton (1959) (Murray Expedition station 24, BMNH 1936.3.4.538): upon re-examination this was found to be dissimilar to Schuffner's description. Burton's specimen (BMNH collection) is hairy due to extending giant diactines and the skeleton is articulated and the atrial skeleton contains tetractines. It is close to and possibly the same species as the above described *Grantessa woerheidei* sp.nov..

Sycon munitum Jenkin, 1908 sensu Burton (1959) (Murray Expedition station 24, nr. 479, BMNH 1938.3.26.29): upon re-examination this appears to be correctly identified by Burton, with brushes of short fat diactines on the distal cones and both triactines and tetractines in the tubar skeleton.

Leuconia wasinensis (Jenkin, 1908) sensu Burton (1959) (Murray Expedition station 45, nr. 537): upon re-examination this does not conform to Jenkin's description of *Leucandra wasinensis* and is likely a member of *Sycettusa simplex* (see Remarks above under *Sycettusa simplex*).

Seychelles and Mascarene Islands

***Asclatis compacta* Schuffner, 1877**

Schuffner's description (1877: 404, pl. 25 fig. 9) points towards *Arturia* or *Ernstia*. It is obviously close to *Arturia sueziana* Klautau & Valentine, 2003, but these authors pointed out that Schuffner's drawing does not show the presence of water-collecting tubes, which are so characteristic of *A. sueziana*. The additional argument for specific distinction, viz. the greater size of the actines of the triactines and tetractines, is not very convincing. In the absence of the type, which appears to be lost, it seems best to reassign *A. compacta* to *Arturia* as *Arturia compacta*.

***Leucosolenia gardineri* Dendy, 1913**

Dendy (1913: 2) extensively described this species from the Chagos Archipelago. It forms lobose masses of tightly anastomosed tubuli measuring 2.5 x 1.5 cm. There are pseudopores at the surface leading to pseudatria. The

spicules include two size categories of triactines (140 x 12 µm and 74 x 7 µm) and one category of tetractines with apical actines of 50 µm. The species is currently assigned to *Ascaltis*.

***Dendya prolifera* Dendy, 1913**

Dendy (1913: 6) described this species from the Amirante Islands, Seychelles. The species has been extensively discussed by Borojević & Boury-Esnault (1986: 445–447). It is a soft wide tube characterized by lateral diverticules. Spicules comprise two categories of triactines (270 x 10 µm and 120 x 8.5 µm) and tetractines with apical actines of 99 µm. The species is currently assigned to *Levinella*. The collection of the Naturalis Biodiversity Center contains a slide, ZMA.POR.P.1170, which is assignable to the genus *Levinella*. Locality Seychelles, N of Aride Island, depth 55 m, Netherlands Indian Ocean Project, 19 December, 1992.

***Leucascus simplex* sensu Dendy 1913**

Dendy (1913: 9) reported his South Australian species (originally described by Dendy 1892) from Providence Island, N of Madagascar. The type material from South Australia has been recently redescribed by Cavalcanti *et al.* (2013: 277), including also Dendy's (1913) record. For details one is referred to Cavalcanti *et al.* 2013.

***Pericharax peziza* Dendy, 1913**

Dendy (1913: 15) described this from Cargados Carajos as a species similar in spiculation to *P. orientalis* (as *P. heteroraphis*), but with a cup-shaped form, size 3.7 cm diameter and a height of the cup of 2.9 cm. The cup walls are 0.7 cm in thickness and are smooth, unfurrowed. Burton (1963) synonymized the two, but Van Soest & De Voogd (2015) considered it a separate species, following Dendy's decision. The inside of the cup has numerous oscular openings. The giant triactines have actines of 1400 x 70 µm, small choanosomal triactines have actines of 180 x 5 µm, cortical triactines are 100 x 5.5 µm, tetractines of the surfaces of the inner wall and canals up to 290 x 12 µm, apical actines slightly crooked, up to 75 µm.

***Sycandra tabulata* Schuffner, 1877**

Schuffner (1877: 422, pl. 25 fig. 11) described this *Sycon* species from Mauritius, comparing it with *Sycon elegans* (Bowerbank, 1845). Its skeleton is distinct only by the thick bushes of thin fusiform diactines (140 x 4 µm) in the distal cones of the radial tubes. Borojević (1967) in turn compared his record of *Sycon elegans* from South Africa with Schuffner's species. Since *S. elegans* is a Northeast Atlantic species, this may be interpreted as a suggestion that the South African record may indeed be better assigned to *Sycon tabulatum*. Schuffner's combination is preoccupied: it is a junior primary homonym of *Sycandra tabulata* Haeckel, 1872. Dendy & Row (1913) noticed this already, but assumed both homonyms belonged to *Sycon elegans*. In view of the fact that Bowerbank's and Haeckel's specimens were from the Mediterranean, while Schuffner's was from Mauritius this synonymy is judged to be unlikely. We propose here to rename Schuffner's species as *Sycon oscari* **nom.nov.** The name is given to honor Oscar Schuffner, the author of its original name.

***Leucandra echinata* Schuffner, 1877**

Schuffner (1877: 411, pl. 24 fig. 4) described a sycon-like individual from Mauritius, with diactines of 1000–2000 x 50–80 µm, triactines up to 309 x 20 µm (smaller of about 110 µm were also present), tetractines with basal actines 110 x 18 µm and apical actines 40 x 9 µm. This species has been interpreted differently by various authors. See for a review Burton (1963: 30 and 248). Ridley (1884: 630) reported a specimen of Schuffner's species (as *Leuconia*) from D'Arros Island in the Amirantes, but failed to present a description or illustration. Dendy (1913: 23) reporting the species from Cargados Carajos also omitted a description, but provided a photo (his pl. 2 fig. 4) of an alleged specimen of *L. echinata*. A secondary homonymy has been caused by Dendy's (1913) suggestion that Carter's (1886) Southeast Australian *Leuconia echinata* could be a synonym of Schuffner's species (indicated with a question mark), in the process reassigning Carter's species to *Leucandra*. Burton (l.c.) was not in accord with this and assigned the two as different 'named species' to different 'superspecies' (our term for Burton's misguided concept of species in the Calcarea), viz. *Leuconia barbata* for Carter's species and *Scypha ciliata* for Schuffner's species. Re-examination of Schuffner's and Carter's material is ultimately necessary to find the proper genus affiliation for Schuffner's species. For the time being, *Leucandra echinata* appears the most proper combination as it is the original combination. Our material did not contain a likely member of Schuffner's species.

***Leucandra claviformis* Schuffner, 1877**

Schuffner (1877: 414, pl. 24 fig. 5) described this sycon-like individual from Mauritius. It possesses diactines of 270–400 x 31 µm and only small triactines and tetractines with actines of 150–160 x 9 µm, with the apical actines of the tetractines 9–40 µm long. These small spicule sizes distinguish this species from most other *Leucandra* species of the region.

***Leucandra falcigera* Schuffner, 1877**

Schuffner (1877: 416, pl. 25 fig. 6) described a tiny oval individual with short apical fringe from Mauritius. The spicule package is similar to that of *L. claviformis*, but the measurements of the actines have a distinctly larger range: the diactines are up to 900 µm, triactines have actines 54–409 x 9–40 µm, tetractines have basal actines 136–227 x 13, with apical actines up to 40 µm long. These measurements are rather similar to those of *L. pilula* sp.nov., but this species lacks the diactines.

***Leucandra seychellensis* Hôzawa, 1940**

Hôzawa (1940: 158) described an oval specimen of 3 cm high from the Seychelles. It has as its most prominent feature giant oxeas of 800–1500 x 45–65 µm arranged scattered irregularly and tangentially over the surface. The main skeleton is a confused arrangement of triactines of 70–260 x 6–30 µm and tetractines of similar size with apical actines 50 x 14 µm. The atrial skeleton consists of sagittal triactines with larger paired actines (130–180 x 8–10 µm) and shorter unpaired actines (50–90 x 6–8 µm).

***Sycortis sycilloides* Schuffner, 1877**

This Mauritius species is discussed above as a possible junior synonym of *Sycettusa stauridia* (Haeckel, 1872). It has similar habitus (two coalescent small tubular individuals), but it has the unpaired actines of the subatrial triactines much longer and thicker (600–1000 x 80 µm) than Haeckel's and ours, which measure only 400 x 10–20 µm.

***Leucilla proteus* Dendy, 1913**

Dendy (1913: 26) described this species from the Seychelles as distinct, but very close to *L. australiensis* (Carter, 1886). He suggested that it was possible that the small Seychelles specimens could be juveniles of the Australian species. *L. australiensis* was also reported from Indonesia (cf. Van Soest & De Voogd 2015, p. 95) and from South Africa (Borojević 1967, p. 221). Borojević (1967) and Borojević & Boury-Esnault (1987b) supported Dendy's view and synonymized *L. proteus* with *L. australiensis*, but eventually Borojević *et al.* (2000) reassigned *L. proteus* to *Paraleucilla proteus* as a separate valid species. Above, the species is compared with *Paraleucilla erpenbecki* sp.nov., showing that the differences with that species are considerable.

***Plectoninia hindei* Kirkpatrick, 1900**

Vacelet (1977) reported this Funafuti species from Réunion, one of the Mascarene Islands, in reef tunnels.

East Africa***Clathrina primordialis* sensu Jenkin, 1908**

Jenkin (1908: 436) gave a short description of specimens of *Clathrina* with actines of 160–180 x 16–20 µm. He assigned these to Haeckel's *Clathrina primordialis* (originally as *Ascetta*). This species is reported widely in the literature but it was recently restricted to the Mediterranean (Klautau & Valentine, 2003; Klautau *et al.* 2016). The spicule sizes of Jenkin's material could indicate membership of above described *Clathrina sinusarabica* Klautau & Valentine, 2003, but the short description is insufficient for a definite conclusion.

***Clathrina darwinii* sensu Jenkin 1908**

Jenkin (1908: 436) described and illustrated specimens assigned to Haeckel's *Ascaltis darwinii* from Zanzibar. This record is discussed above in the Remarks on *Arturia sueziana*.

***Clathrina contorta* var. *spinosa* sensu Jenkin 1908**

Jenkin (1908: 437) described three specimens of a pure white sponge from Zanzibar with irregularly anastomosed tubuli under this name. *Leucosolenia contorta* (Bowerbank, 1866) from Northeast European waters has a checkered history (cf. Minchin 1905; Klautau & Valentine 2003) with the current not well-established conclusion that it is a senior synonym of *Ascetta spinosa* Von Lendenfeld, 1891 described from the Adriatic and now assigned to the genus *Ascandra* as *Ascandra contorta* (see Klautau *et al.* 2016). How Jenkin (1908) came to consider his specimens to be a member of this species from Europe is not quite clear. The triactines and basal actines of the tetractines were 80–150 x 10–12 µm, the apical actines of the tetractines were 50–65 x 5–7 µm. It is likely, but not certainly a species of *Ernstia* and its pure white color may indicate it is as yet undescribed.

***Clathrina blanca* sensu Jenkin 1908**

This was discussed above in the Remarks paragraph of *Clathrina* aff. *pulcherrima*

***Leucosolenia irregularis* Jenkin, 1908**

Jenkin (1908: 440, figs 88–90) described this from Wasini Island, near Zanzibar. It has been reassigned to *Soleneiscus* by Borojević *et al.* (2002: 1144). Voigt *et al.* (2017) compared this with his Red Sea *Soleneiscus hamatus*, concluding the two are closely related but separate species.

***Leucilla floridiana* sensu Jenkin 1908**

Jenkin (1908: 453) reported the Central West Atlantic species *Leucetta floridana* (Haeckel, 1872) (originally as *Leucaltis*) from Wasini Island. He misspelled the species name (as *floridiana*) and transferred the species to the genus *Leucilla* because of the presence of ectosomal giant tetractines. Valderrama *et al.* (2009) redescribed and discussed *L. floridana*, restricting the occurrence of that species to the West Atlantic. They pointed out that Jenkin's description is too limited to be able to classify his material and redescription is necessary.

***Sycon ampullum* sensu Jenkin 1908**

Jenkin (1908: 443) described a small *Sycon* specimen under this name from Wasini Island. The name refers to Haeckel's (1872: 308) *Sycandra ampulla*, a species from Brazil. The change of the name to *ampullum* is a mistake, because *ampulla* is a noun that is not be changed with the gender of the genus name. The data he provided are insufficient to characterize the species. Jenkin did not indicate whether it was stalked, the main feature of *Sycon ampulla*, so it will remain unnamed until it is redescribed (see also below under additional species from South Africa)

***Sycon ciliatum* sensu Jenkin 1908**

Jenkin (1908: 442) reported this North Atlantic species, described by Fabricius (1780: 448, as *Spongia*), from Zanzibar without data other than the size (specimens were 8 x 2 and 5 x 1.25 mm). It is unlikely that a species from North Atlantic occurs in tropical East African waters. The species remains unnamed until it is redescribed.

***Sycon munitum* Jenkin, 1908**

Jenkin (1908: 442) extensively described three specimens of this species from Zanzibar. It is characterized by having both tri- and tetractines in the tubar skeleton and the brushes of diactines at the distal cones are long and relatively thin. For details of spicules size one is referred to Jenkin's excellent description. The species is also reported from the South Arabian coast by Burton (1959), cf. above.

***Leucandra ananas* sensu Jenkin 1908**

Jenkin (1908: 444) reported this North Atlantic species, originally described by Montagu (1814: 96, as *Spongia*) from Zanzibar. The sponges were small and flask-shaped. The spicules included long diactines, 700–3000 x 28–46 µm, triactines of the cortex and the main skeleton 180–500 x 5–32 µm, tetractines with basal actines 170–280 x 6–20 µm, apical actines 50 x 6–9 µm. Possibly, one of the species of Schuffner (1877), e.g. *L. echinata* could fit with Jenkin's specimens.

Madagascar

Leucetta primigenia sensu Vacelet & Vasseur 1965

The species is Mediterranean. No description was given of the Madagascar material, except that it was bright yellow in color. This suggests that the record concerns *Leucetta chagosensis*.

Lelapiella incrustans Vacelet, 1977

Vacelet (1977: 358) described this species from reef tunnels off Tuléar, Madagascar.

Calcareous ‘sclerosponges’

Vacelet (1967a, 1967b), Vacelet & Vasseur (1971), Vacelet *et al.* (1976), Vacelet (1977) described and recorded a number of Calcareous with massive basal skeletons from reef tunnels off Tuléar, Madagascar: *Lepidoleucon inflatum* Vacelet, 1967, *Paramurrayona corticata* Vacelet, 1967, *Plectoninia vasseuri* Vacelet, 1967, *P. minima* Vacelet, 1967, *P. pulchella* Vacelet, 1967, *P. radiata* Vacelet, 1967, *P. tecta* Vacelet, 1967, *Tulearinia styliifera* Vacelet, 1977.

South Africa (westward until Port Elizabeth, 25°E)

Clathrina cerebrum sensu Borojević, 1967

Borojević (1967: 192) reported this Mediterranean species, originally described by Haeckel (1872: 54, as *Ascaltis*), from Kwazulu Natal, Eastern South Africa. The Mediterranean species has been reassigned to *Borojevia* by Klautau *et al.* 2016. Like the Mediterranean *B. cerebrum*, Borojević’s specimen has tripods of 60–100 x 20–32 µm, unlike the three *Borojevia* species described above. Like these three species the South African specimen has spined apical actines of the tetractines. This record likely represents an additional undescribed species of *Borojevia*.

Sycon ampulla sensu Borojević, 1967

Borojević (1967: 194) reported the occurrence of this South American species, described by Haeckel (1872: 308, as *Sycandra*), from the southern and eastern coast of South Africa. Like Haeckel’s species this is a stalked *Sycon*. Borojević’s claim that the South African specimens are very similar to the South American specimens cannot be corroborated, as there are clear differences: Haeckel states that the stalk consists mostly of long diactines of up to 1.5 mm long, whereas these of South Africa are only up to 200 µm. The characteristically swollen unpaired actines of the atrial and peduncular tri- and tetractines are not mentioned or pictured by Haeckel. We believe the South African material does not belong to *Sycon ampulla* (Haeckel, 1872).

Sycon elegans sensu Borojević 1967

Borojević (1967: 201) reported this North Atlantic species (cf. Bowerbank, 1864) from the Durban coast, admitting that this was the southernmost occurrence of the species. Simultaneously he referred Burton’s (1933) record of West Pacific *Sycon gelatinosum* (Blainville, 1834) and East African *Sycon tabulatum* (Schuffner, 1877) to the very similar *S. elegans*. As we pointed out above, *Sycon tabulatum* appears the more likely identity for this record, as *S. elegans* and *S. gelatinosum* have their type localities at a great distance from East Africa.

Sycon natalense Borojević, 1967

Borojević (1967: 200) described this very characteristic species from the Natal coast. It has a peculiar arrangement of the diactines at the distal cones, not in a brush as is usual, but arranged along the distal part of the radiating tubes. Additionally, the subatral tri- and tetractines have the paired actines strongly different in length, which is very characteristic. For further detail see Borojević’s description and illustrations.

Leuconia armata Urban, 1908

This was described by Urban (1908: 24) and found again by Brøndsted (1931: 38) and Borojević (1967) along the eastern and southern coasts of South Africa. The species is a *Leucandra* with as most characteristic feature microdiactines surrounding single large diactines protruding from the surface. For more details of *Leucandra armata* see Borojević (1967).

***Leuconia glomerosa* Bowerbank, 1873**

Bowerbank (1873: 17) described a mass of coalesced tubes from Port Elizabeth. Subsequently, this same species was found in Western India, described by Dendy (1916) and in West Australia (Row & Hôzawa 1931, not described). The skeleton is inarticulate and the spicules include a sheath of cortical giant diactines underneath a thin layer of small triactines, and supported by subcortical pseudosagittal triactines. The tubar skeleton is formed by the longest actine of the subcortical triactines and the unpaired actines of atrial triactines. The atrial skeleton consists mostly of triactines, but there are also relatively rare tetractines. The species has been reassigned to *Heteropia glomerosa* by Dendy (1916).

***Grantessa ramosa* sensu Borojević 1967**

Borojević (1967: 204) assigned specimens from Natal (along with specimens from more westward coasts of South Africa) to Haeckel's (1872) *Sycandra ramosa*. This was originally described likewise from South Africa, including Natal. Haeckel's description and drawings (p. 358, pl. 54 fig.1, 58 fig. 8) and those of Borojević do not resemble each other very well. Borojević's assumption that Haeckel failed to recognize or draw pseudosagittal subcortical triactines remains uncorroborated.

Discussion and conclusion

With the above results, biodiscovery of Calcarea of the Western Indian Ocean received a great boost, not only by adding at least 16 new species to the known fauna, but also by providing more extensive and precise delimitation of many already known species. A great help in achieving these results was the use of molecular sequences. The Calcarea 'barcode', the C2–D2 region of the 28S ribosomal RNA gene, proposed by Voigt & Wörheide (2016), appears to 'work' in many cases by providing independent markers for species that are recognized by ambiguous, variable or indistinct morphological features. We studied a few of such cases, e.g. *Clathrina luteoculcitella* and *C. rowi*, or *Sycettusa hastifera* and *Sycettusa hirsutissima* **sp.nov.**, by comparing aligned sequences of these closely related species and examining the occurrence of consistent site differences. This provides additional confidence in decisions about species distinctness.

The database for the Calcarea barcode is growing, especially in the Calcinea where most genera are already represented by one or more species sequences. This is necessary for a successful use of the barcode in the taxonomy of Calcarea, confirming species identities and assignment of new species to their proper genus. Improvements are still urgent, as not all type species of the genera have been included, rendering molecular characterization of genera uncertain. In Calcaronea, the database is still lagging behind, barcodes of many genera and even whole families are still not represented in GenBank or in the Sponge Barcoding Project, often preventing proper use of the sequences in molecular taxonomy of these groups.

Regrettably, we were not in all cases successful in obtaining these barcodes, rendering the classification of some specimens possibly doubtful. On the other hand, we added over 120 new partial 28SrRNA sequences including for the first time pivotal taxa such as *Kebira* (two species).

Of course, barcodes, including the one of Voigt & Wörheide (2016), by its rather short sequence length could have a restricted phylogenetic use, and may not be expected to always 'work' at the family or deeper levels, evidenced by our Phylogeny of the Calcaronea (Fig. 3), which showed several 'inexplicable' discrepancies with the Systema Porifera classification of the subclass (Borojević *et al.* 2002b). Other genes or longer sequences may need to be employed for phylogeny of higher taxa. Some studies, e.g. Manuel *et al.* 2003, Dohrmann *et al.* 2006, Voigt *et al.* 2012, have attempted to draw an outline of the phylogeny of the whole class Calcarea, but the limited taxon content of these studies did not provide more substance than the realization that morphology at the family and suborder level probably does not always represent the true phylogenetic relationships. More detailed studies at the genus and family level, for example the one of Klautau *et al.* 2013 on Clathrinidae, are necessary to build a new framework for the classification of the Calcarea.

The Calcarea fauna of the Western Indian Ocean and the Red Sea is still far from comprehensively known. Recent collecting activities by us were not exclusively directed to Calcarea, and most specimens were collected along with the other Porifera groups. This is reflected by the apparent lack or rarity of species of common genera as *Ascandra*, *Leucosolenia*, *Sycon*, or *Leucilla*. We refrain from speculating how many species are still to be discovered in this large region.

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